Ecology of the tawny owl *Strix aluco* in the spruce forests of Northumberland and Argyll

Thesis

ECOLOGY OF THE TAWNY OWL *STRIX ALUCO* IN THE SPRUCE FORESTS OF NORTHUMBERLAND AND ARGYLL

STEPHEN JOHN PETTY

Submitted for the degree of Doctor of Philosophy in Biology

The Open University

December 1992

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ABSTRACT

The ecology of the tawny owl was studied in the man-made spruce forests of Kielder, Northumberland (1980-91) and Glenbranter, Argyll (1984-91). Kielder was drier, colder and less mountainous than Glenbranter. Field voles were the main food of tawny owls in both forests. Vole populations exhibited a three-year cycle of abundance in Kielder but showed less variability and were generally less plentiful in Glenbranter. Tawny owls obtained most of their voles from clear-felled areas but used older growth stages in the forest for roosting and nesting. Owl territories were regularly distributed along valleys, with density declining at higher elevations. The numbers of territories increased during the study, probably due to clear-felling which resulted in more food. All aspects of reproduction were significantly related to vole abundance. In Glenbranter compared to Kielder, tawny owls bred at a lower density, territories had a higher occupancy rate with less variation in the proportion of pairs breeding, and on average fewer chicks fledged per pair. In Kielder, most tawny owls failed to breed every third year when vole numbers were low. Without the demands of a family, both male and female owls replaced many more wing feathers than in years when chicks were reared. Population turnover was investigated in Kielder. Here tawny owls showed a high degree of fidelity to their territories and had a high annual survival (84-85%). The median natal dispersal distance was 3.05 km for both males and females, with 30% settling to breed no more than two territories from where they were reared, although none bred in its natal territory. About 80% of chicks recruited into the breeding population were reared in years when vole populations were increasing. There were unoccupied territories in every year studied, and recruitment into the breeding population was the main factor limiting the growth of the population to 4.5% per annum.

ACKNOWLEDGEMENTS

My interest in bird ecology had lain dormant for a number of years until the late Judith Rowe, Wildlife Research Officer for the Forestry Commission offered me a job. She encouraged me to develop bird-related studies and gave support and effective criticism during those formative years. She also encouraged me to start on the path that led to this thesis. Sadly she died before it was completed.

Two people are responsible for my love of owls. First I met Mick Marquiss. His knowledge, enthusiasm, and friendship kindled in me an interest in raptors that has persisted through the years. Mick encouraged me to work on sparrowhawks when I lived in Kielder Forest, and because I did, I soon met Ian Newton. After getting to know the forest and most sparrowhawk nests over a number of years, I increasingly became aware of the presence of tawny owls. These were the main cause of breeding failure in sparrowhawks, because they occasionally killed adults at the nest. My interest in tawny owls might easily have stopped there, but Ian Newton had the foresight to suggest that I would learn far more about tawny owls than sparrowhawks. How right he was! Since then he has been a source of encouragement and a constructive critic of my work. I was delighted when he agreed to be my external supervisor. In this role he has given me much support and has carefully read and made valuable comments on two drafts of all chapters.

David Anderson helped tremendously with the fieldwork, particularly in the latter part of the study. His lively sense of humour has many times brought me back to reality. I have had unbelievably few complaints after suggesting a normal fieldwork day in the spring starts at first light by emptying male owl traps, and finishing only when he was unable to see to reset any more traps in the evening! I have greatly valued his friendship throughout this study.

Diane Chadwick diligently word processed the whole of my thesis without one complaint. Anyone with any knowledge of my hand-writing will have nothing but admiration for such a feat!

I thank Paddy Maher my internal supervisor for steering me through the Open University system and for his comments on all chapters.

I have also had much support from colleagues in the Forestry Commission's Research Division. Phil Ratcliffe took over from Judy Rowe and continued to encourage my work. Andy Peace provided sound advice about how my analyses could be improved. However, any errors that remain are entirely my own! Staff in the library at Alice Holt have provided a superb service over the years. George Gate has prepared some of the illustrations and many superb colour data slides for various talks I have given.

Staff in the Forest Districts have tolerated my activities with few complaints! I offer my thanks especially to Bob Selmes and latterly Angus Murray in Cowal Forest District and Bob McIntosh, Bill Boulton, Gordon Riley and David Jardine in Kielder Forest District. I am grateful to the Northumbrian Water Authority for allowing me to site nestboxes on their land. The Nature Conservancy Council (as it was) and the British Trust for Ornithology kindly supplied the licenses for my work. Many other people have also helped.

Finally, my wife Linda has given me tremendous support and the encouragement necessary to complete the thesis. This has involved many sacrifices, including three weeks of my annual leave for each of the last three years. Linda has also helped with fieldwork and read and corrected my grammar in all chapters. This thesis has also been my excuse for totally avoiding any jobs to be done in the house or garden. The day of reckoning is nigh!

CONTENTS

LIST OF FIGURES

LIST OF PLATES

INTRODUCTION

Background

Objectives

Organisation of the thesis

Statistical methods

INTRODUCTION

Background

In the last 70 years, large areas of the British uplands have been planted with exotic conifers, and spruces *Picea* spp. have been increasingly used (Anon 1984a, Petty and Avery 1990). Most crops are grown on short rotations of 45-55 years and many of the earlier plantings are now being clear-felled and replanted (restocked). Clear-felling provides foresters with an opportunity to alter spatial patterns within forests. Recently much effort has been directed towards making these vast areas, which were often planted over a short period, into more attractive habitats. This is being achieved largely by shortening and advancing rotation lengths and felling areas much smaller than the initial plantings, to create a finer-grained patchwork of different-aged stands of trees (Hibberd 1985; Ratcliffe and Petty 1986). Very little is known about how wildlife adjusts to such changes.

A number of studies have examined the effects of afforestation of open ground on raptors (for reviews see Newton 1983; Ratcliffe and Petty 1986; Petty 1988), but little is known about how birds of prey react to restocking, or about the ecology of tawny owls in these extensive man-made forests. Tawny owls colonise spruce forests once the structure is open enough to allow the owls to fly between the trees. This usually occurs 20-25 years after planting.

Objectives

This study aimed to:

A. Investigate the population ecology of tawny owls in upland spruce forests by taking measurements of density, fecundity, immigration, emigration and mortality.

B. Examine these demographic variables in relation to food supply, and also other environmental variables, such as weather.

C. Determine how tawny owl populations are limited in spruce forests.

Organisation of the thesis

The thesis comprises eight chapters. Chapter 1 presents a brief account of tawny owl biology and distribution. Chapter 2 describes the climate, physical aspects and habitat of the two study areas. Chapters 3-7 form the core of the thesis, presenting work on diet (Chapter 3), distribution (Chapter 4), reproduction (Chapter 5), population turnover (Chapter 6) and moult (Chapter 7). Chapter 8 draws together the results from previous chapters to explore how tawny owl populations are limited in this man-made habitat. Scientific names of plants and animals are given at their first mention in each chapter.

Statistical methods

Most of the statistical analyses were done with Statgraphics version 4.0 (Statistical Graphics Corporation, USA), a statistical and graphics package designed for use on personal computers. Statgraphics was also used to produce most of the figures.

The probability threshold for rejecting a null hypothesis was 5% ($P=0.05$). Increasing significant differences were indicated by $P<0.05$(*), $P<0.01$(**) and $P<0.001$(***). A probability of $P<0.1$ was sometimes used to indicate a non-significant trend. All statistical tests were two-tailed unless otherwise stated. Parametric tests were used with data that were normally distributed and non-parametric tests for data that were not (or not known to be) normally distributed. Chi-squared tests used the actual data values and not percentage values, and all regression analyses were done using the least squares method. The following notations were used:

n = number of units in a sample

SD = estimate of the population standard deviation from a sample

SE = standard error of the mean

P = probability

r = product moment correlation coefficient of a sample

r-squared = coefficient of determination

rs = Spearman rank correlation coefficient

a = intercept of a regression line on the Y axis

b = regression coefficent (or slope)

t = test statistic for t test

F = test statistic for F test

NS = not significant

CHAPTER 1

THE TAWNY OWL - A SHORT REVIEW

1.1 Introduction

1.2 Size

1.3 Colour phases

1.4 Vision and hearing

1.5 Food and hunting methods

1.6 Annual cycle

1.7 Distribution of the tawny owl and closely related species

1.1 Introduction

This chapter provides a brief account of tawny owl *Strix aluco* biology and distribution. It is not a comprehensive review of the literature, but helps to set the scene for the main part of the thesis.

1.2 Size

The British and west European race of the tawny owl (*S.a.sylvatica*) is the smallest in Europe, with north and east European races becoming increasingly larger (Table 1.1). These trends conform with Bergmann's rule of increased body size to the north of a species range. Five species of owl regularly occur in Britain of which the tawny owl is the largest (Table 1.2). Female tawny owls are on average larger than males, although there is an over-lap between small females and large males. Hardy *et al.* (1981b) found female winglength to be 4.3% longer and body weight 26.2% heavier than males. This is a common trend amongst raptors (Newton 1979), although in some owls (mainly in the genus *Ninox*) from the southern hemisphere males are the larger sex (Olsen 1991). The degree of sexual size dimorphism in tawny owls is greater than in the other species of owls in Britain, but it is far less than in the highly dimorphic diurnal raptor the sparrowhawk (*Accipiter nisus*). Comparable dimorphism indices for winglength (female/male) are 1.04 for tawny owls (Table 1.2) and 1.19 for sparrowhawk (Newton 1986).

The tawny owl appears dumpy and short-winged compared to the barn *Tyto alba*, long-eared *Asio otus* and short-eared *Asio flammeus*, the other owls widely distributed in the British uplands. This is reflected in its higher wing loading, making hunting in flight less efficient than from perches, although it uses both tactics (Nilsson 1978). Short wings give manoeuvrability in woodland but the relatively high weight makes sustained flight costly. These morphological characteristics and the constraints and advantages they impose have evolved for life in woodland. In contrast, the

Table 1.1 Comparison of winglength mm range (mean) n of races of tawny owls in western Eurasia, quoted in Mikkola (1983) and Cramp (1985) both of whom use other sources).

Race	Females	Males
sylvatica (England)	255-272 (267) 32	248-268 (257) 47
aluco (Netherlands)	263-287 (276) 44	253-275 (265) 49
aluco (E.Germany)	266-299 (280) 18	261-284 (271) 25
aluco (Sweden)	272-298 (284) 25	265-283 (274) 25
wilkonskii (Caucasus)	282-305 (296) 33	266-296 (276) 17
aluco (W USSR)	277-311 (296) 65	268-295 (283) 53
siberiae (NE USSR)	301-307 (303) 3	280-300 (290) 4

Table 1.2 Biometrics from five species of owl occurring in Britain (from Mikkola 1983 and Cramp 1985)

Biometric	Tawny owl	Short-eared owl	Long-eared owl	Barn owl	Little owl
Wing loading (g/cm^2)	0.40	0.34	0.31	0.29	-
Male weights	352-465 (409)20	286-350 (324) 7	221-303 (256)21	250-400 (292)12	142-193 (162) 9
Female weight	435-716 (533)22	280-425 (350)10	262-435 (308)21	252-330 (296)11	148-188 (166)12
Dimorphism index (weight)	1.30	1.08	1.20	1.02	1.02
Male winglength	248-268 (257)47	304-326 (315)39	282-310 (294)57	279-299 (289)18	158-169 (163)13
Female winglength	255-272 (267)32	309-331 (319)28	287-309 (299)64	280-300 (290)13	161-173 (166)13
Dimorphism index (winglength)	1.04	1.01	1.02	1.00	1.02

Biometrics are taken from British owls, where these are not available then data from the Netherlands are used. Weights (g) and winglengths (mm) give range (mean) n. Weights are from the period October - March except for tawny owls which are from the entire year. Dimorphism indices are female/male weight or winglength.

three other species of owls hunt mainly on the wing, over open country, and the two *Asio* owls can migrate/disperse large distances (Cramp 1985).

1.3 Colour phases

There is a gradation in the background colour of the plumage from grey through to reddy-brown (Cramp 1985; Voous 1988). Grey morphs are reputed to predominate in colder, northern regions and brown morphs in more southerly areas. This fits Gloger's ecogeographical rule which states that animals in warm and humid areas are more heavily pigmented than those in cool and dry areas, and black pigments are reduced in warm dry areas while brown pigments are reduced in cold humid areas (Mayr 1965).

1.4 Vision and hearing

Tawny owls are mainly nocturnal, although they will hunt throughout the day when chicks are being fed in the nest (Mikkola 1983; Cramp 1985). Martin (1982; 1986) has shown that tawny owls have an average visual sensitivity about 2.5-fold higher than the average man. This difference lies within the normal range of absolute visual sensitivity in humans, so some humans may see better than some owls. Owls do not have a visual acuity far superior to humans as was once believed. For example, in average light conditions in broadleaved woodland at night, a small rodent walking across snow would be invisible to owl and man at a distance greater than about 3 m.

Tawny owls locate their prey mainly by ear. The outer ears are large and asymmetrical in size, shape and position. Auditory sensitivity appears to be similar to humans (Martin 1986; Norberg 1977; 1987). However, one advantage of asymmetrical ears is that horizontal and vertical direction of sound can be determined simultaneously with the same accuracy in both planes (Norberg 1987). The position of moving prey in dense vegetation can thus be continuously monitored. This suggests that tawny owls locate,

attack and catch prey largely by sound and may be unaware of its identity until after capture (Nishimura and Abe 1988).

1.5 Food and hunting methods

A powerful build combined with strong legs and talons enables the tawny owl to kill prey almost as large as itself, up to around 500 g, such as woodpigeons *Columbus palumbus*, part-grown rabbits *Oryctolagus cuniculus* and red squirrels *Sciurus vulgaris* (Cramp 1985). Even small raptors, such as sparrowhawk, kestrel *Falco tinnunculus* and little owl *Athene noctua*, can be killed (Mikkola 1983). However, within any area, diet largely reflects the abundance and vulnerability of different prey species. Small mammals feature prominently, particularly in the northern part of the tawny owls range in Europe, including Britain (Cramp 1985). In broadleaved woodland, wood mice *Apodemus sylvaticus* and bank voles *Clethrionomys glareolus* are important prey, whereas in open areas field voles *Microtus agrestis* are taken more frequently. Birds can form an important part of the diet, particularly in urban areas (Harrison 1960) and amphibians and arthropods (particularly earthworms) are also taken (Cramp 1985).

Pronounced seasonal and annual shifts in diet occur, as the relative abundances of different prey species change. For example, a number of studies have shown that small mammals are important early in the breeding season, but birds (particularly recently fledged juveniles) and young rabbits are taken later in the season. Diet has been well-studied, and good summaries appear in Glutz and Bauer (1980), Mikkola (1983) and Cramp (1985).

Tawny owls hunt mainly from perches where they sit and locate prey by sound. Prey capture is usually achieved with a short glide from the perch. They also hunt in flight over open areas lacking perches (Cramp 1985; Nilsson 1979). Nishimura and Abe (1988) explored hunting strategies of captive Ural owls using live mice *Apodemus speciosus* and *A.argenteus* and voles *Microtus montebelli*. They

demonstrated that owls attacked prey at random, but caught more *Microtus*, because they were less agile than *Apodemus*. They also showed that the owls increased their prey capture rates in poor feeding conditions. Tawny owl may behave similarly, as they hunt in the same way as Ural owls.

1.6 Annual cycle

Tawny owls are highly territorial, and boundaries between adjacent pairs are asserted vocally in September-October, when juveniles of the year are dispersing and trying to locate vacant territories, and then again in January and February just prior to breeding (Figure 1.1) (Southern 1970; Hirons 1976). They have a wide repertoire of calls; the males territorial "hooting" and the females "kewick" are most frequently heard, but boundary disputes can result in a surprising range of screams and wails (Anderson 1961; Wendland 1963; Cramp 1985). Both Hirons (1976) and Southern (1970) considered that food ultimately determined the density of breeding pairs, with territorial behaviour being the proximate mechanism.

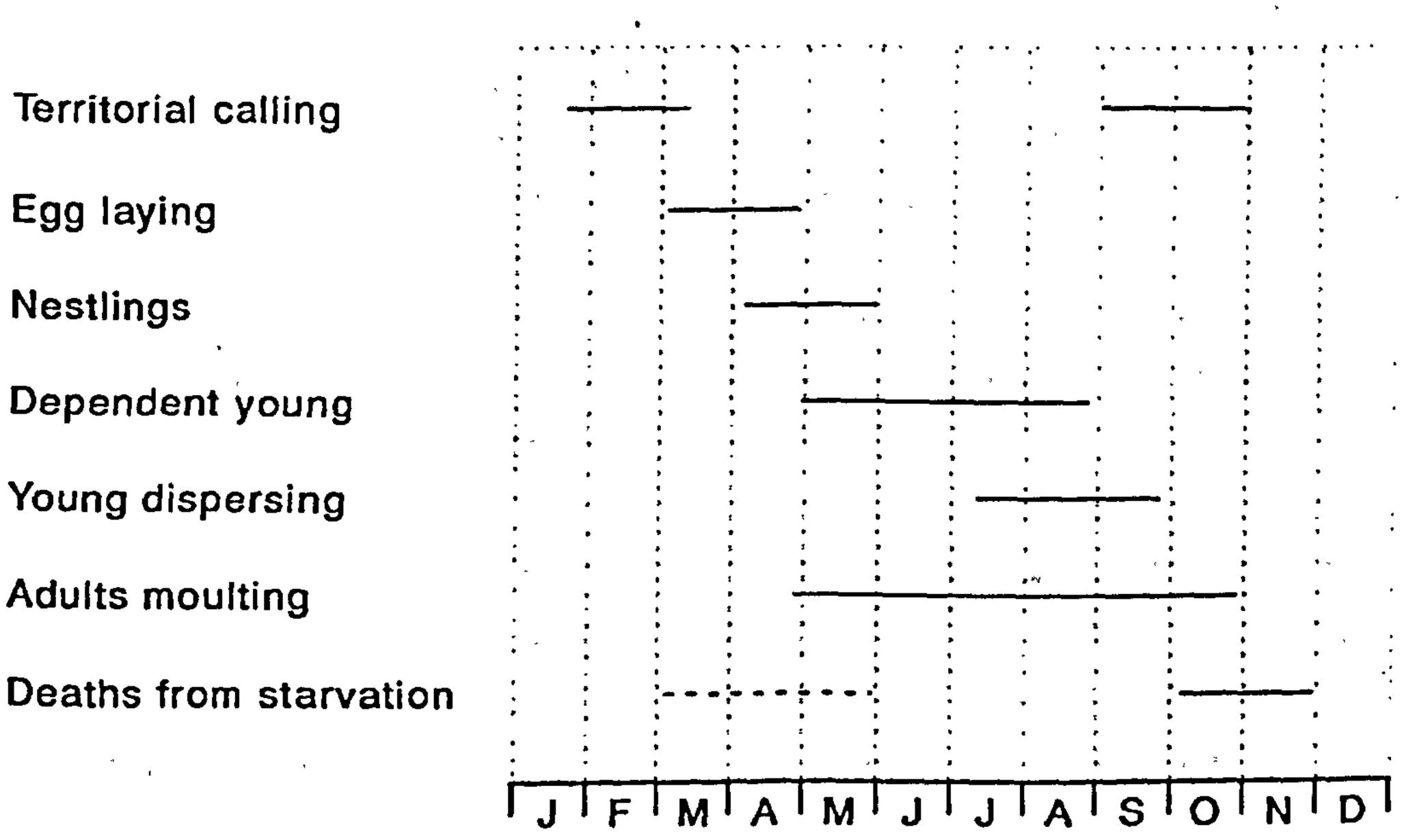


Figure 1.1 Summary of the major events in a tawny owl's year (data from Hardy et al. 1981, Hirons et al. 1984 and Cramp 1985).

Male and female increasingly roost together prior to egg laying and the male gradually does more of the hunting. He feeds the female in early spring, enabling her to substantially increase her body weight and produce eggs. Those females which do not increase their body mass sufficiently, due to poor food supply or inability of the male to provide food, fail to lay (Hirons 1976, Hirons 1985a).

Tawny owls do not build their own nests, but are dependent on other structures or substrates in which to breed. When the favoured tree cavities are not available they will use a great variety of other sites, including disused stick nests of squirrel, crow and buzzard for instance, or disused buildings or crag ledges. They will even nest on the ground at the base of a tree if nothing else is available (Cramp 1985).

In Britain eggs are laid mainly in March and April. Within the same area, the timing of egg-laying varies greatly between years, depending largely on food supply, although above average temperatures in the winter may also promote early laying (Hirons 1976). Clutch sizes vary between two and five eggs, with one and six eggs also recorded, but much less frequently. Hirons (1976) gave a mean clutch size of 2.70 (SD=0.81) eggs and a mean brood size for successful nests at fledging of 1.99 (SD=0.75) chicks for Britain, based on Nest Record Cards from the British Trust for Ornithology during 1947-1972. Large differences in the number of chicks reared between years in the same area are associated with variations in prey abundance (Southern 1970).

During breeding the sexes have different roles, with the female tending the eggs and chicks and the male providing the food. The female starts hunting again in the latter part of the nestling period. The chicks leave the nest (fledge) when 28-32 days old and spend a further 10 weeks or so in their parents' territory while still dependent on their parents for food (Southern 1970; Cramp 1985). This is considerably longer than any other diurnal or

nocturnal raptor of similar body size in Britain. Juveniles disperse from their natal territory from mid-July onwards, and many die before their first winter.

Moulting is the other major nutritional constraint for the tawny owl. Adults which successfully rear young start to moult soon after the chicks fledge and usually stop by the end of September, even though not all feathers have been replaced. Birds which fail in a breeding attempt appear to start moulting earlier (Hirons *et al.* 1984; Cramp 1985).

1.7 Distribution of the tawny owl and closely related species

The tawny owl is widely distributed in Europe and Asia (Figure 1.2). It occurs largely in temperate broadleaved and mixed conifer/broadleaved forests, but also extends southwards into mediterranean and northwards into boreal zones (Mikkola 1983; Cramp 1985; Voous 1988). It is one of four widely distributed and largely sedentary wood owls (genus *Strix*) in the Holarctic region; the barred *Strix varia* and spotted owl *Strix occidentalis* in North America, and Ural and tawny owl in Europe and Asia (Figure 1.2).

Another *Strix* owl with a wide circumpolar distribution in the northern hemisphere is the great grey owl *Strix nebulosa* (Cramp 1985). However, in many aspects of its life style it is quite distinct from the other four *Strix* owls mentioned above (Voous 1988). Great grey owls are more nomadic with a life history akin to another group of owls that are dependent on vole and lemming cycles. These include short-eared owl, snowy owl *Nyctea scandiaca* and hawk owl *Surnia ulula* (Cramp 1985).

In Europe the tawny owl substantially expanded its range northwards in the 1920's and 1930's (Merikallio 1958). In Finland this expansion largely occurred in broadleaved forests in coastal and

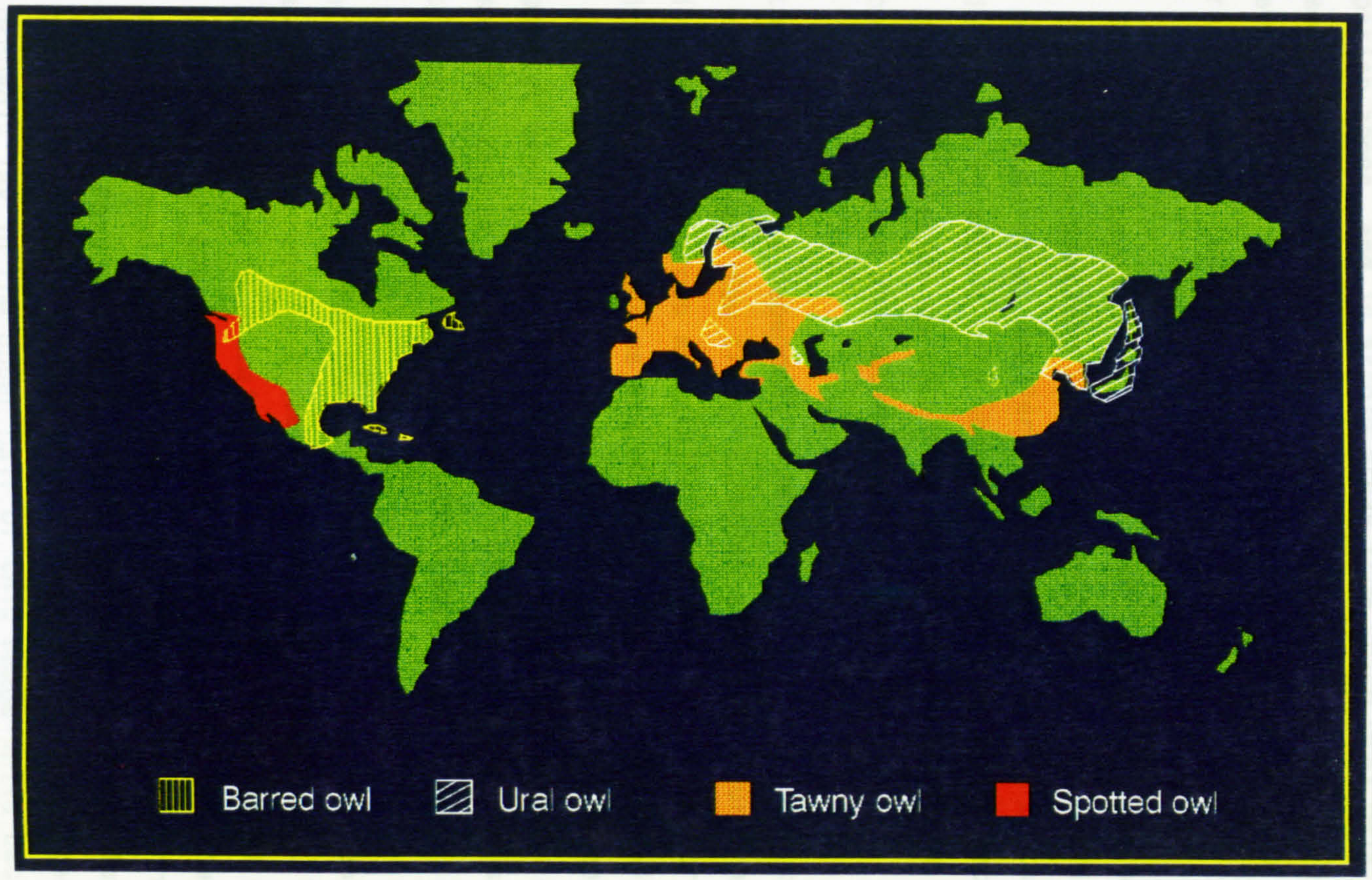


Figure 1.2 World distribution of the four most widely distributed, sedentary wood owls of the genus Strix in the Holarctic region (redrawn from Voous 1988).

riparian zones, and in arable areas from which Ural owls were absent. Competition from Ural owls appears to be one factor preventing tawny owls from colonizing coniferous forests in northern Europe (Lundberg 1980).

In Britain the tawny owl is widely distributed but does not occur in Ireland, the Shetland Isles, Orkney Isles, Outer Hebrides, Isle of Man and some other smaller island groups. On the British mainland it is absent only where trees are completely lacking, such as some upland areas particularly in north-west Scotland, and the flows of Caithness and Sutherland (Sharrock 1976).

Although primarily dependent on woodland, the tawny owl can exist in areas with very few trees. Examples are agricultural areas where buildings or hedgerows are utilized and hill areas in northern Britain where territories are centred on steep ravines with few or no trees, where the birds nest in cavities in scree or on well vegetated crag ledges. In addition tawny owls have shown a remarkable degree of adaptation in colonizing urban and suburban habitats, breeding in buildings and trees.

The tawny owl is by far the most abundant of five species of owl that regularly breed in Britain and Ireland (Table 1.3). The *Atlas of Breeding Birds in Britain and Ireland* (Sharrock 1976) recorded it as present in 60% and confirmed breeding in 46% of the 3862 10-km squares covered by the Atlas. This includes Ireland from where it is absent. Parslow (1973) estimated the British population to be in the range 10,000-100,000 pairs. Sharrock (1976) suggested that it probably lay in the upper half of this range while Lack (1986) thought the winter population could be as high as 35,000-350,000 individuals. Due to its nocturnal habits it is not an easy bird to count, so an accurate estimate of its breeding population is unlikely to be achieved.

Table 1.3 The presence of five species of owl by 10-Km squares in Britain and Ireland during 1968-72 (Sharrock 1976).

Species	Number (%) of 10-Km squares		Estimated population range(pairs)
	Present	Confirmed breeding	
Tawny owl	2305(60%)	1793(46%)	10,000-100,000
Barn owl	2279(59%)	1380(36%)	4,500-9,000
Little owl	1381(36%0	940(24%)	7,000-14,000
Long-eared owl	942(24%)	497(13%0	3,000-10,000
Short-eared owl	802(21%)	369(10%)	1,000+
Snowy owl	5(<1%)	1(<1%)	-

There are 3862 10-km squares in Britain and Ireland

Parslow (1973) suggested that tawny owl numbers had declined in the 19th century due to persecution, largely by gamekeepers on many of the large estates that flourished at the time. A general increase appears to have taken place between 1900 and 1950, but both Parslow (1973) and Sharrock (1976) considered that population size had remained largely unchanged in recent years, while Marchant *et al.* (1990) suggested that numbers were higher in the late 1960's and early 1970's compared to later years. Prestt (1965) recorded small local declines in the period 1953-1963 coinciding with the use of organochlorine pesticide in agricultural areas. However, Cooke *et al.* (1982) recorded low levels of residues from these chemicals in tawny owls compared to bird-eating raptors such as sparrowhawk, merlin *Falco columbarius* and peregrine *Falco peregrinus*.

Since the formation of the Forestry Commission in 1919, over one million ha of new forest has been established, much of this since the Second World War. This has inevitably led to a substancial increase in the range and numbers of tawny owls, particularly in the uplands, as these new forests have reached maturity.

CHAPTER 2

STUDY AREAS

2.1 Introduction

2.2 Physical characteristics

2.2.1 Kielder

2.2.2 Glenbranter

2.3 Climate

2.3.1 Rainfall

2.3.2 Temperature

2.4 Forest and other habitats

2.4.1 Tree species and age distribution

2.4.2 Forest succession

2.5 Summary

2.1 Introduction

Two forests were selected for study (Figure 2.1), both owned by the Forestry Commission. Kielder (55° 15' N, 2° 35' W) was situated in the centre of Kielder Forest District, Northumberland, in north-east England (Figure 2.2). Glenbranter (56° 05' N, 4° 58' W) was 180 km north-west of Kielder, in Cowal Forest District, Argyll, west Scotland (Figure 2.3). This chapter describes the physical characteristics, the climate and the forests of these areas as a basis for the chapters that follow.

2.2 Physical characteristics

While both study areas could be described as "upland" in nature, they differed in many respects so their physical characteristics are described separately.

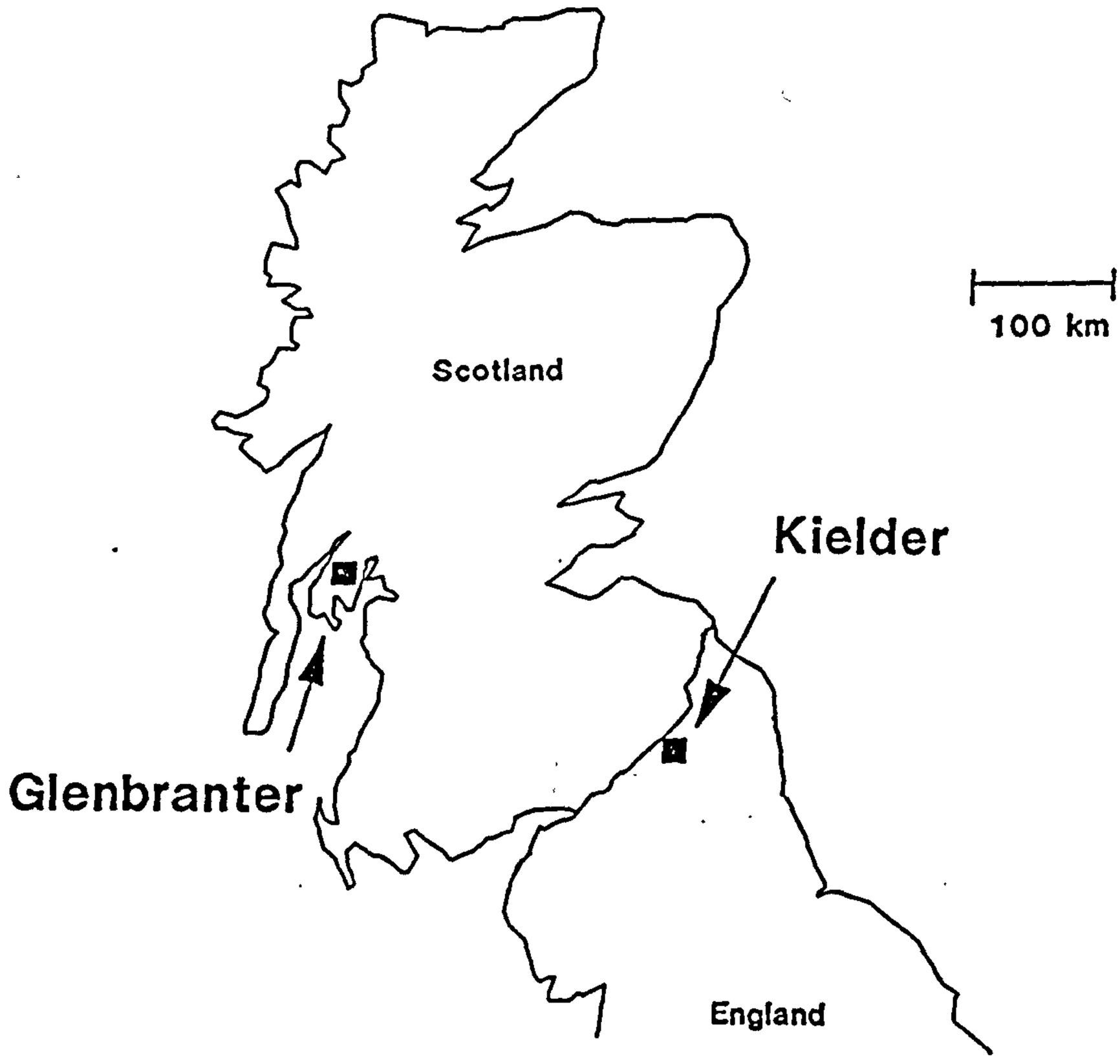


Figure 2.1 Location of the Kielder and Glenbranter study areas.

Figure 2.2 The location of the Kielder study area in Northumberland. The blue grid is at 10 km intervals. The extent of the study area is indicated by the dashed lines which encloses 180 square km. A black star shows the location of the meteorological station at Kielder Castle.

Figure 2.3 The location of the Glenbranter study area in Argyll. The blue grid is at 10 km intervals. The extent of the study area is indicated by the dashed lines which encloses 175 square km. Black stars show the location of the meteorological stations at Benmore and Ardentinny.

2.2.1 Kielder

The Kielder study area lies mid-way between the Solway Firth on the west coast and the North Sea on the east coast (Figure 2.1). The north-west corner extends a little into Scotland, the rest is in south-west Northumberland in England (Figure 2.2). It is situated entirely in the upper valley of the River North Tyne. In 1981-82, 1000 ha of the valley below 185 m above sea level (ASL) was flooded to form Kielder Water Reservoir. The altitudinal range therefore extends from 185 m on the shores of Kielder Water to the summit of Deadwater Fell at 569 m, a southern extremity of Kielderhead Moor lying to the north of the study area.

The topography is one of gently rolling hills with higher, unplanted moorlands surrounding the study area to the south-west, north-west and north-east. A number of large streams flow into Kielder Water and it is along their eroded valleys that most rocky outcrops occur (Plates 2.1 and 2.2).

The solid geology is mainly sedimentary derived from the Lower Carboniferous series (Robson 1965). Fell Sandstones form most of the higher ground around the upper catchment of the River North Tyne. Under the Fell Sandstones lie the Cementstones which form the lower ground towards the north. Both of these groups lie on top of the Scremerstone Coal Group which comprises the southern half of the study area. The Cementstones and Scremerstone Groups include base-rich layers of shales and limestones, while the latter group also has coal seams. In the past both coal and limestone were mined in the area.

As the glaciers melted at the end of the last ice age, large amounts of glacial drift (boulder clay) were deposited over most of the study area concealing much of the solid geology. The main exceptions were the higher moors and the upper hill slopes, and where the action of water has eroded these glacial deposits.

Plate 2.1 The gentle terrain of the Kielder study area looking south down the North Tyne Valley. Kielder Water is in the centre.

Plate 2.2 The Kielder study area showing one of the main stream systems (Kielder Burn) in the north.

2.2.2 Glenbranter

The Glenbranter study area is situated on the Cowal peninsula in south Argyll, Scotland (Figure 2.1). The Firth of Clyde and Loch Long form a sea barrier to the south and east as does Loch Fyne to the north and west. The study area extends across the width of the peninsula from Loch Long to Loch Fyne and includes the mountains on either side of a valley system containing the fresh water Loch Eck (Figure 2.3). The altitudinal range is greater than in Kielder, from sea-level to 779 m on Beinn Bheula in the north-west of the area.

The topography is mountainous with steep, often craggy hillsides, and deep glacial valleys (Plates 2.3 and 2.4).

The solid geology comprises metamorphic rocks belonging to the Dalraidian system which occupy most of Scotland between the Great Glen Fault and the Highland Boundary Fault (Johnstone 1966; Whittow 1977). The Highland Boundary Fault lies just to the south of the study area.

The rocks are of various kinds but fall into two main groups, schistose grits and mica-schists. Both have base-rich layers. The rugged grandeur of the area owes much to a folding of the earth surface resulting in the Cowal Anticline and subsequent glacial activity gouging-out deep U-shaped valleys. Unlike Kielder, the glacial deposits are less regular, less deep, and less compacted.

2.3 Climate

Meteorological data were taken from the *Monthly Weather Report* and *Annual Weather Report* published by the Meteorological Office. Four meteorological stations were situated within or near the two study areas.

Kielder Castle at 201 m ASL was at the northern end of the Kielder study area (Figure 2.2). Many weather data were missing from Kielder Castle, so when investigating monthly and annual trends,

Plate 2.3 The rugged terrain of the Glenbranter study area looking north up Loch Eck.

Plate 2.4 The Glenbranter study area north of Loch Eck, looking north-east across the main valley towards Invernoaden.

the sample size was often less than for the meteorological stations in Glenbranter. To overcome this, data from another meteorological station were used, namely Redesdale (235 m ASL, grid reference NY 834955) 20 km east of Kielder Castle.

Ardentinny (Outdoor Centre) and Benmore (Younger Botanical Gardens), at 5 m and 12 m ASL respectively, were located towards the southern end of the Glenbranter study area. Ardentinny was on the side of Loch Long (a sea loch) while Benmore was further inland (Figure 2.3). There was little difference in the meteorological data between these two stations, so data from Benmore only were used.

The years 1979 to 1990 (inclusive) were used to calculate annual weather statistics, and the months August 1978 to April 1991 were used to calculate monthly weather statistics. These weather data span the period when tawny owls were studied in Kielder (1979-1991) but include more years than the study (1984-1991) in Glenbranter.

2.3.1 Rainfall

The main climatic difference between Glenbranter and Kielder was in rainfall. In Glenbranter little difference in rainfall occurred between the two meteorological stations as both had an annual mean of nearly 2500 mm, in contrast to Kielder with 1420 mm and Redesdale with 934 mm (Table 2.1).

There were annual variations in rainfall, with Glenbranter consistently having more than Kielder, and Kielder more than Redesdale. There were no apparent trends for annual rainfall to either increase or decrease during 1979-1990 (Figure 2.4). However, there was a pronounced seasonal trend in both Kielder, Redesdale and Glenbranter (Figure 2.5). The driest month of the year in each study area was April, with May, June and July only slightly wetter. In the four driest months (April to July), the difference between Kielder and Glenbranter was least pronounced, although Glenbranter was still wetter than Kielder. These four months (April-July) span

Table 2.1 Annual weather statistics from two meteorological stations (Ardentinny and Benmore) in the Glenbranter study area, one in the Kielder study area (Kielder) and and one in the valley system east of Kielder (Redesdale). The data given are, mean (number of years) SE.

Parameter	Ardentinny	Benmore	Kielder	Redesdale
Mean daily max. temp. 0^C	12.1(10)0.15	11.8(12)0.17	11.0(4)0.35	10.4(10)0.22
Mean daily min. temp. 0^C	5.2(11)0.16	5.1(12)0.15	3.2(5)0.23	3.5(11)0.24
Mean daily temp. 0^C	8.6(10)0.16	8.5(12)0.15	7.2(3)0.44	7.0(10)0.19
Annual rainfall mm.	2482(11)89.9	2462(12)72.0	1420(9)48.5	934(12)29.5
1.0 mm of rain or more (days)	206(11)3.93	211(12)3.32	185(9)4.02	157(12)3.94
Snow lying at 09.00hrs. (days)	13.9(9)2.86	19.6(12)3.02	40.6(8)7.35	36.1(12)5.96
Air frost (days)	50.4(11)4.86	58.5(12)4.69	107.8(5)9.65	84.0(11)5.68

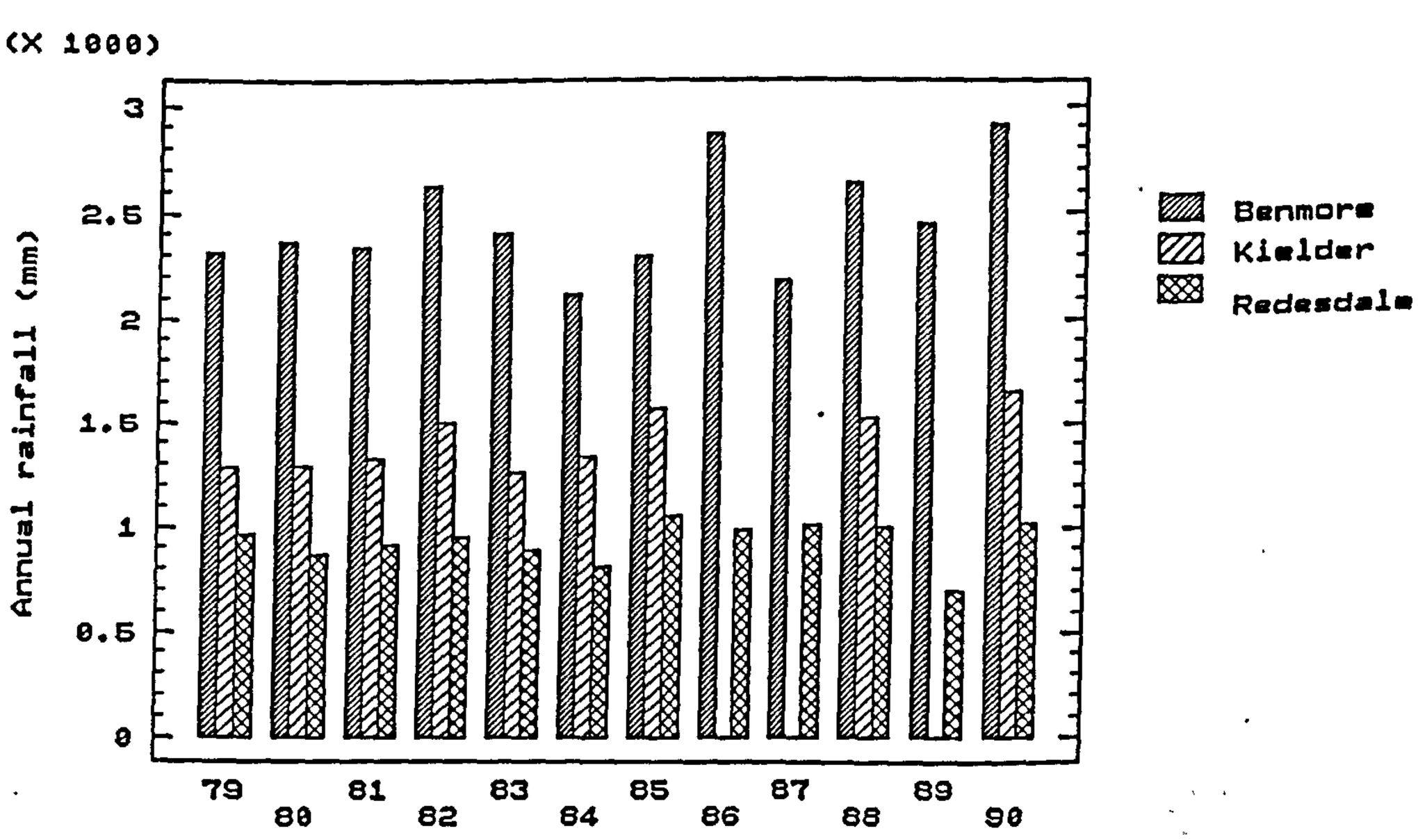


Figure 2.4 Total rainfall each year from 1979 to 1990 from meteorological stations at Benmore (Glenbranter), Kielder and Redesdale.

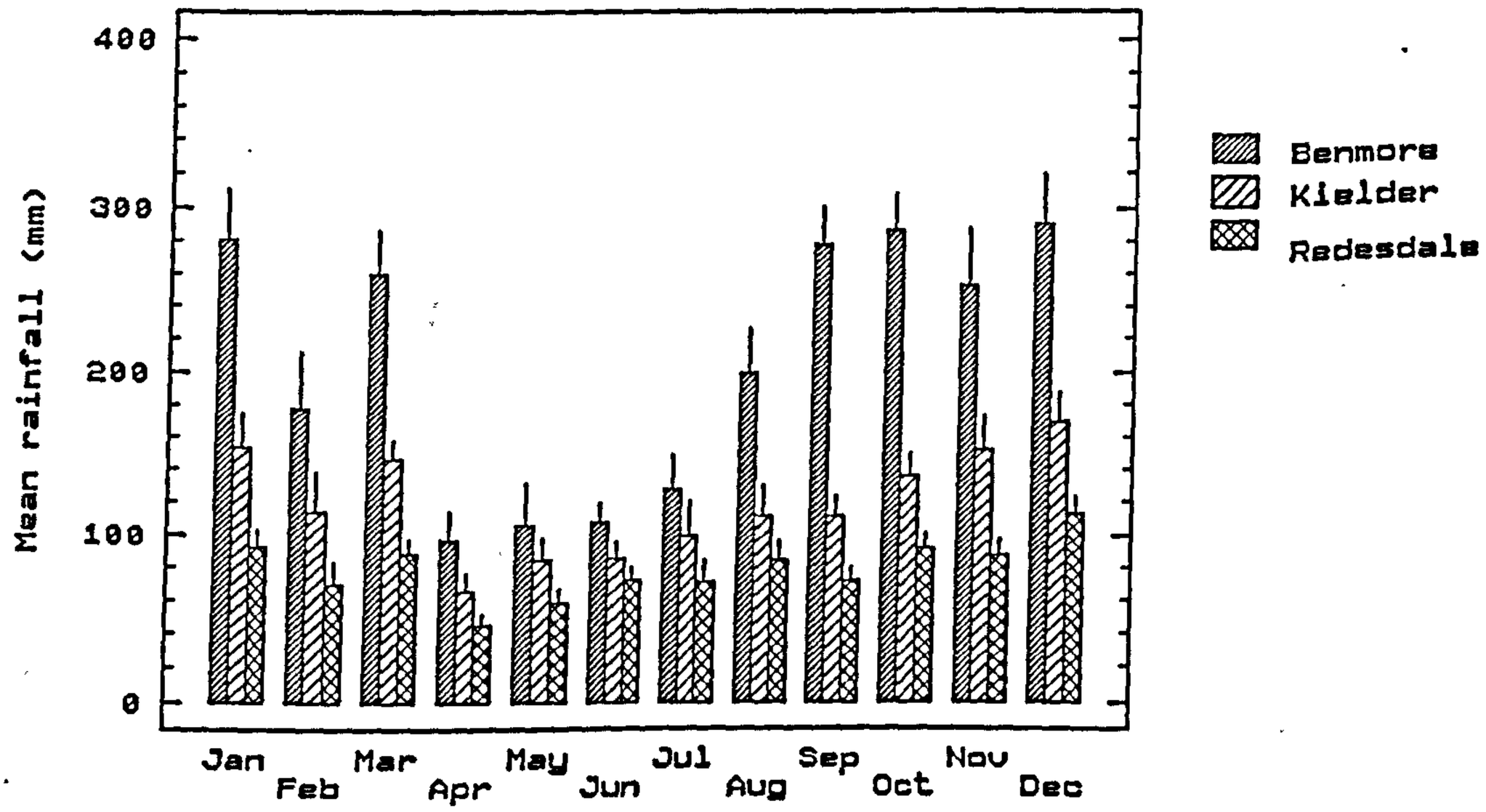


Figure 2.5 Total rainfall (mean with SE bars) each month over a 13-year period from meteorological stations at Benmore (Glenbranter), Kielder and Redesdale.

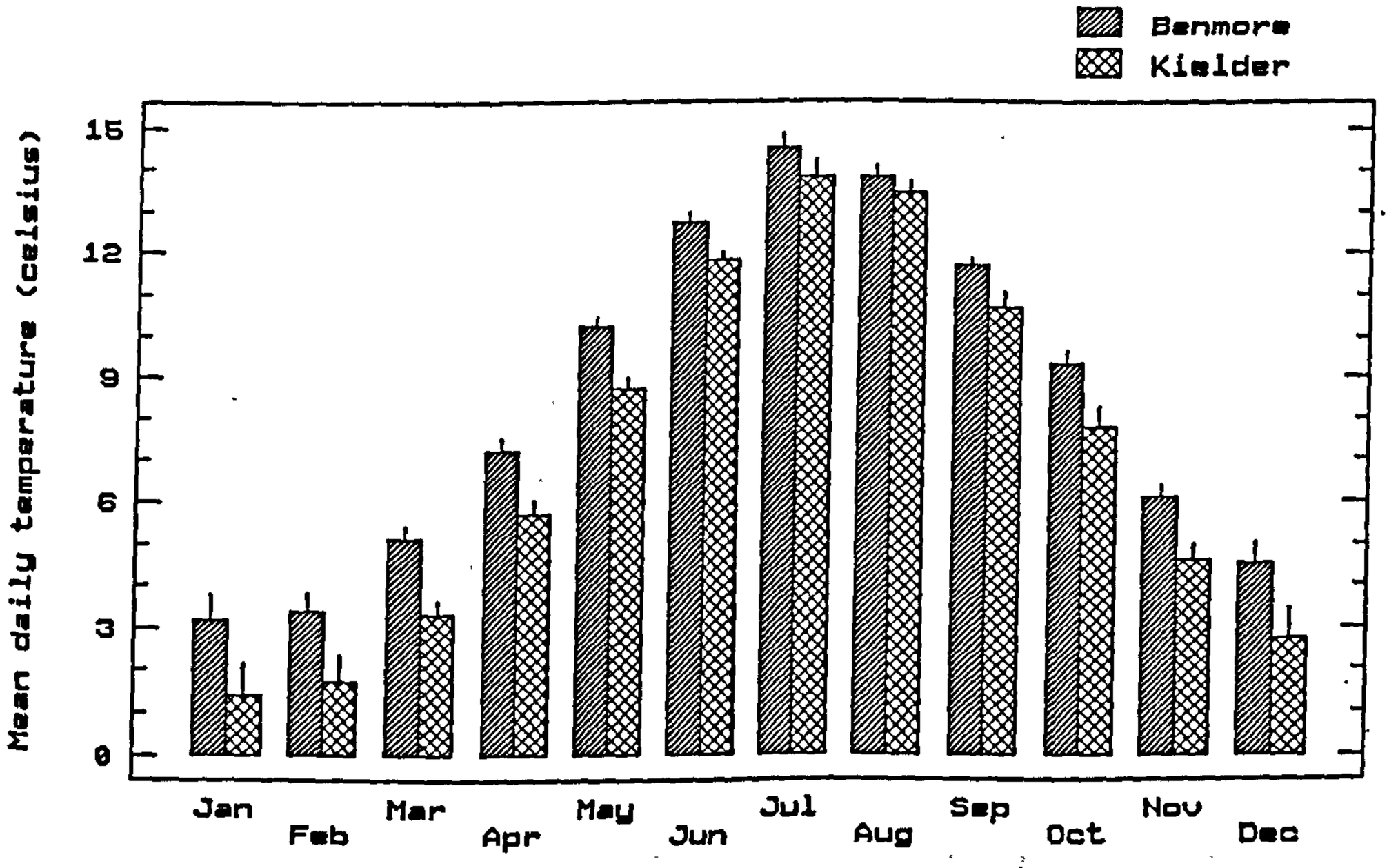
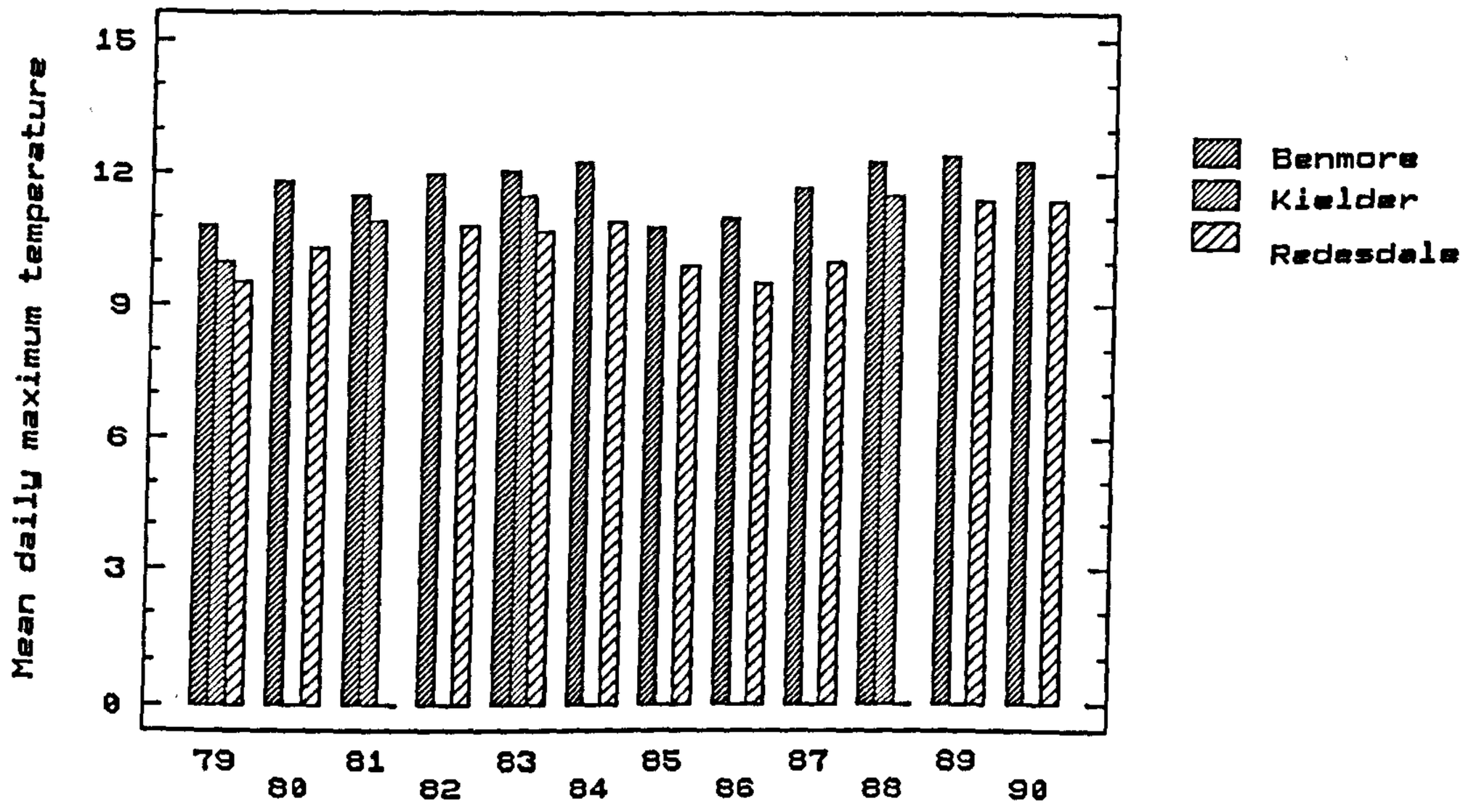


Figure 2.6 Mean daily temperature (celsius) averaged over a 13-year period (with SE bars) from meteorological stations at Benmore (Glenbranter) and Kielder.



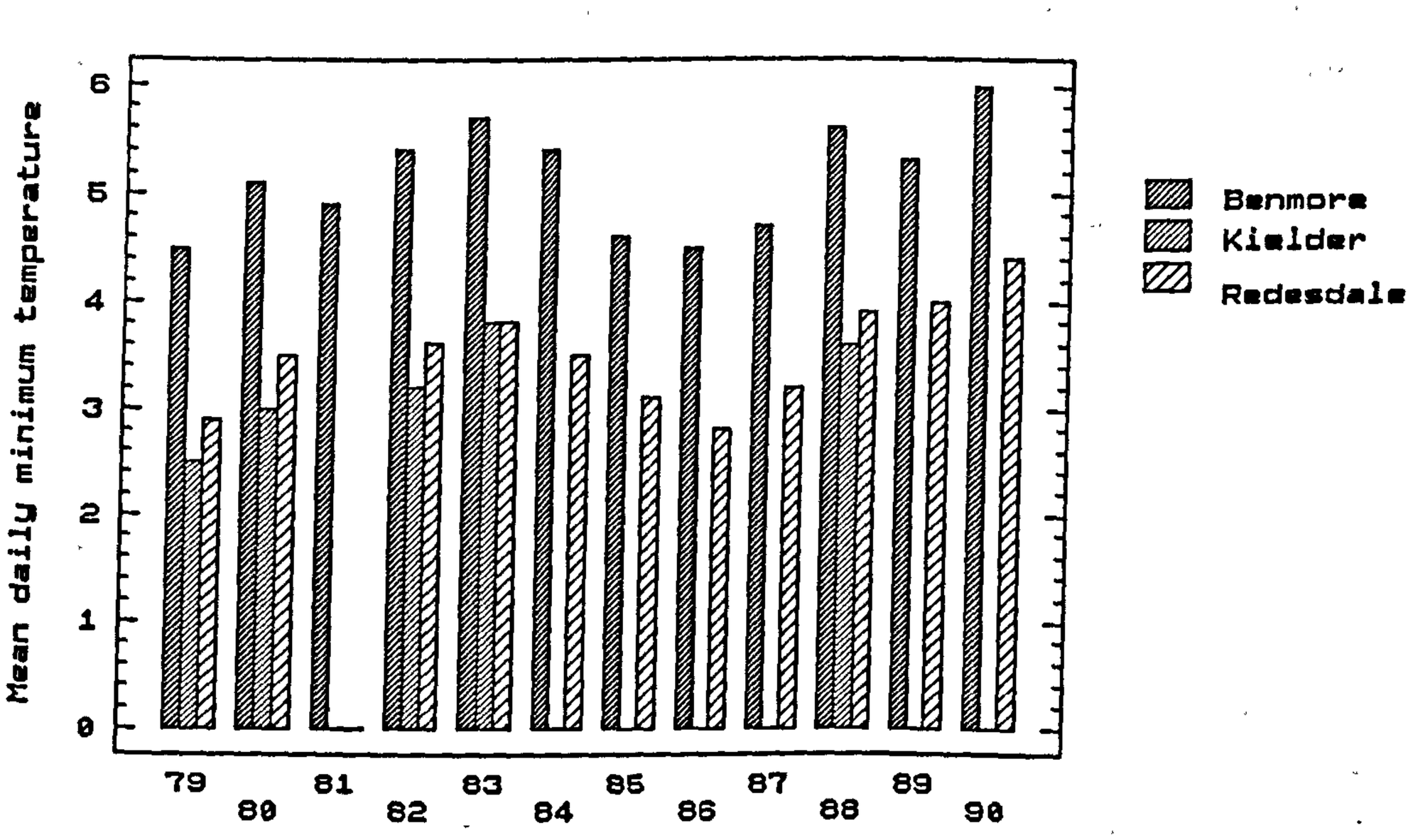


Figure 2.7 Mean daily maximum temperature (celsius) each year from 1979 to 1990 (above) and mean daily minimum temperature for the same period (below) from meteorological stations at Benmore (Glenbranter), Kielder and Redesdale.

most of the breeding season for the tawny owl, although egg-laying can start in March when food is abundant (Chapter 1). For the remaining months (August to March), Glenbranter received about twice the rainfall of Kielder.

2.3.2 Temperature

July was the warmest month of the year and January the coldest (Figure 2.6). Monthly mean daily temperature trends were similar in both Kielder and Glenbranter (Benmore), with least difference in temperature between the study areas in the summer and most in the winter.

The mean daily maximum temperature, both overall (Table 2.1) and annually (Figure 2.7 upper), showed far less variation between the weather stations in Glenbranter, Kielder and Redesdale than did mean daily minimum temperature (Figure 2.7 lower). The minimum temperatures were considerably higher in Glenbranter. Minimum temperatures also showed more annual variation than did maximum temperature, with a relatively higher minimum temperature in 1982-

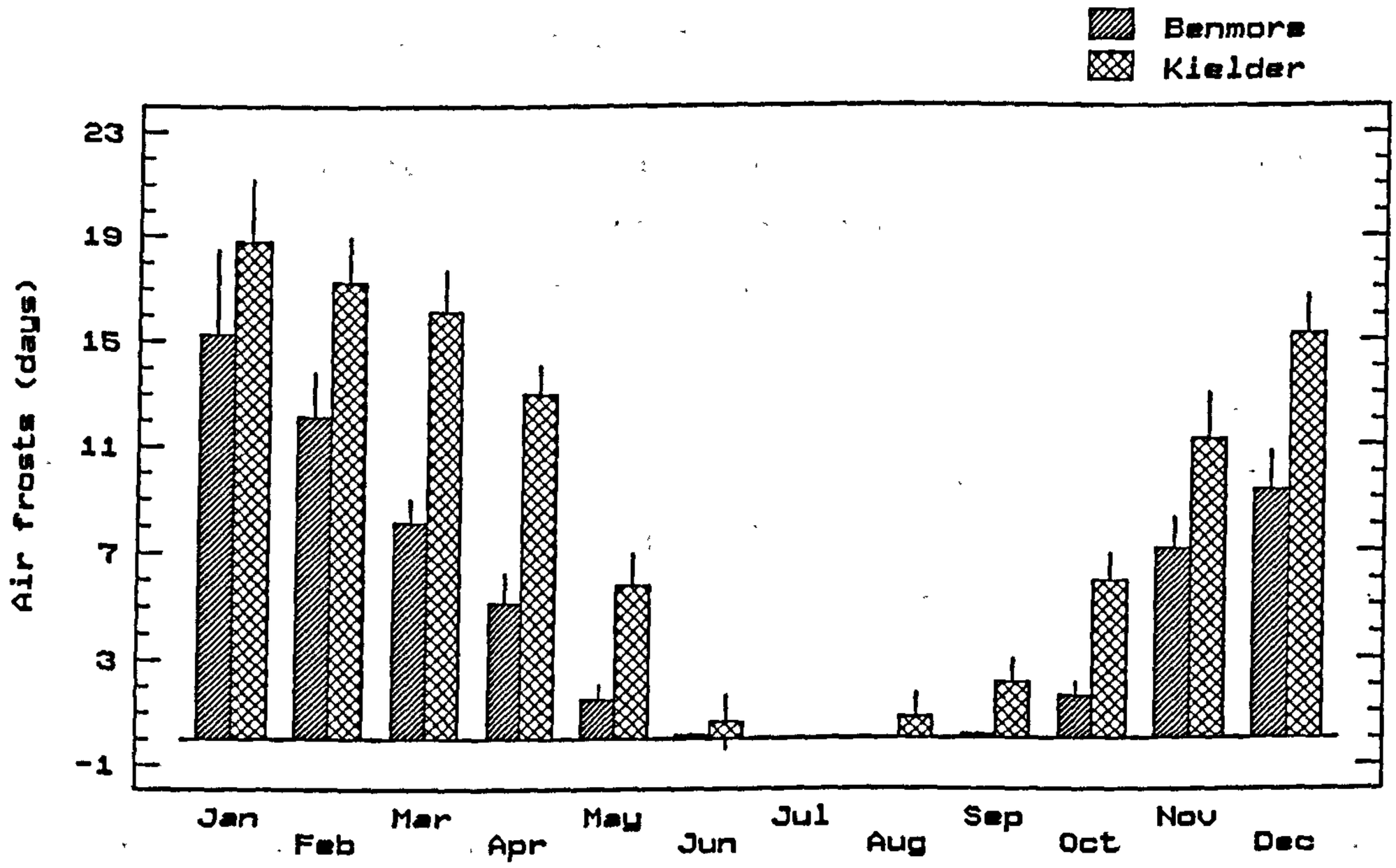


Figure 2.8 Days with air frosts per month averaged over a 13-year period (with SE bars) from meteorological stations at Benmore (Glenbranter) and Kielder.

1984 and 1988-1990 and lower ones in 1985-1987 and prior to 1980. These trends in minimum temperature were common to all three weather stations (Figure 2.7 lower).

Other weather data available were also related to coldness. These were the number of days with air frosts and the number of days with snow lying at 09.00 hrs (Table 2.1). The only frost-free months were July in Kielder and July and August in Glenbranter (Figure 2.8). Most frost days occurred in January with substantially more in Kielder than Glenbranter. Inspection of annual variations in the number of days with air frosts and days with snow lying, suggest that both have declined from 1979 to 1990, but with a slight upward surge in the mid to late 1980s (Figure 2.9).

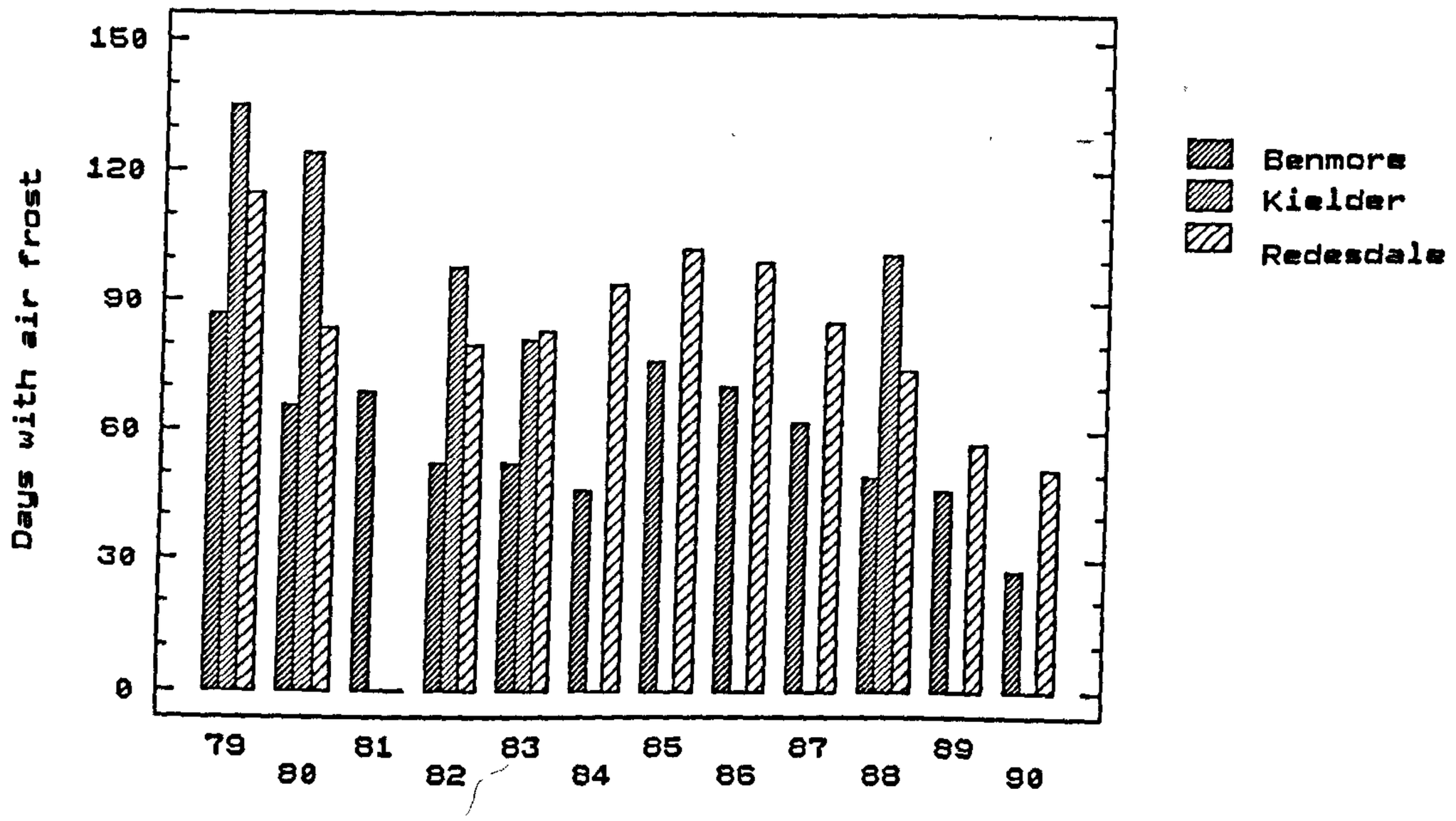
2.4 Forest and other habitats

Both study areas were used extensively for sheep grazing prior to the Forestry Commission acquiring the land. Remnants of natural woodland persisted on steep slopes along burns and on crags protected from felling and fire. More broadleaved woodland survived in Glenbranter because it was steeper than Kielder, and because oak woods were managed for charcoal production and leather tanning. Sheep grazing still persists on some unplanted areas in both study areas, both on high moorlands and enclosed fields in the valleys. But some of the higher mountain areas and moorlands are now ungrazed by domestic stock and are managed primarily for wildlife.

The boundary of each study area enclosed the outermost pairs of tawny owls (Chapter 4). Both study areas were a similar size (Figures 2.2 and 2.3) but Glenbranter included more water and non-forested ground. Only 17% of Glenbranter was forested compared to 63% of Kielder.

2.4.1 Tree species and age distribution

The tree species composition of each study area was similar (Table 2.2). None of the coniferous trees planted were native to either area. Sitka spruce *Picea sitchensis* comprised 75% of the forest



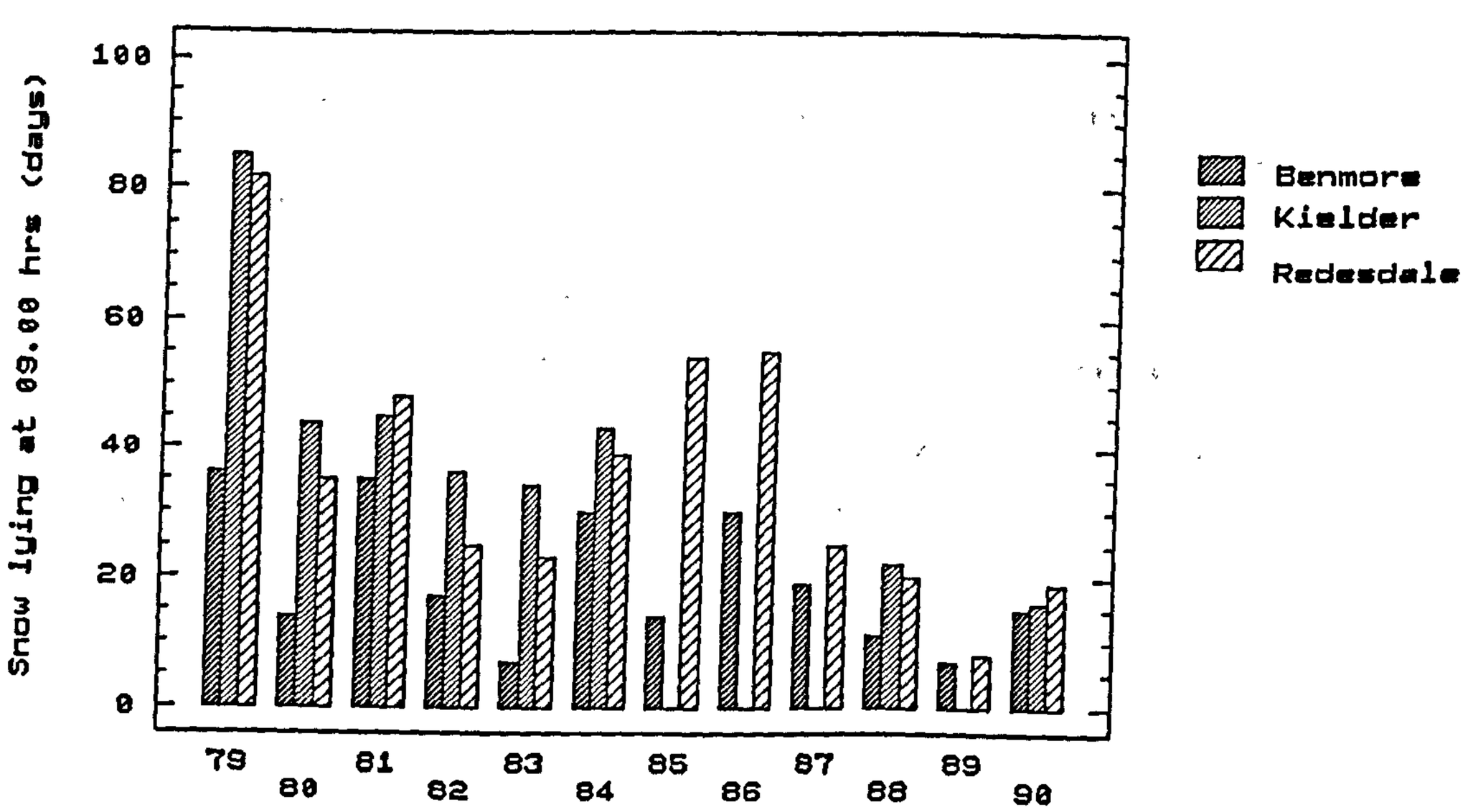


Figure 2.9 Days with air frosts each year between 1979 and 1990 (upper) and days with snow lying at 09.00 hrs. during the same period (lower) from meteorological stations at Benmore (Glenbranter), Kielder and Redesdale.

Table 2.2 Tree species composition of the two study areas in 1990. Figures 2.2 and 2.3 show the study area boundaries.

Tree species	Kielder		Glenbranter	
	area(ha)	%	area(ha)	%
Sitka spruce	8498.1	75.0	2584.5	88.2
Norway spruce	1632.8	14.4	148.3	5.1
Scots pine	168.0	1.5	3.0	0.1
Lodgepole pine	784.0	6.9	9.5	0.3
Larch	192.8	1.7	114.5	3.9
Douglas fir	25.5	0.2	33.0	1.1
Other conifers	33.0	0.3	28.4	1.0
Broadleaves	1.0	<0.1	8.0	0.3
Total	11335.2	100.0	2929.2	100.0

Larch includes Japanese and hybrid larch in Kielder, and these plus European larch in Glenbranter.

Other conifers includes conifer mixtures.

Table 2.3 Age class distribution of crops in the two study areas in 1990. Figures 2.2 and 2.3 show the study area boundaries.

Planting year classes	Kielder		Glenbranter	
	area(ha)	%	area(ha)	%
Pre 1921	15.0	0.1	0.5	<0.1
1921-1930	0.0	0.0	150.0	5.1
1931-1940	1425.7	12.6	158.5	5.4
1941-1950	2511.4	22.2	167.3	5.7
1951-1960	3401.8	30.0	211.5	7.3
1961-1970	1273.5	11.2	527.0	18.1
1971-1980	1417.8	12.5	821.5	28.1
1981-1990	1290.0	11.4	885.0	30.3
Total	11335.2	100.0	2921.3	100.0

area in Glenbranter and 88% in Kielder. Kielder had disproportionally more Norway spruce *Picea abies*, lodgepole pine *Pinus contorta* and Scots pine *Pinus sylvestris* but less larch *Larix spp.* Other tree species were insignificant in both areas. Planting with conifers started in Glenbranter in 1921 and in Kielder in 1933 and was mainly finished in both areas by 1980. Felling and replanting (restocking) commenced after a particularly severe gale in January 1968 which resulted in extensive windthrow in many upland forests (Holtam 1971). Restocking is now a major operation in both study areas with currently over 1000 ha per annum being felled and replanted in Kielder Forest District and over 200 ha in Cowal Forest District (Chapter 3, Table 3.14).

Relatively more of the forest in Kielder was planted in the three decades 1931-40, 1941-50 and 1951-60 (Table 2.3). Most of Glenbranter was younger, with proportionally more planted in the three later decades, 1961-70, 1971-80 and 1981-90.

2.4.2 Forest succession

Sitka spruce grows fast compared to many other trees. This results in rapid habitat changes over a short period. The various successional stages in a forest rotation are important to wildlife as different wildlife communities are associated with each stage (Moss 1978; Moss 1979; Moss *et al.* 1979; Hill 1979; Ratcliffe and Petty 1986; Good *et al.* no date; Wallace 1992). There is general agreement on the definition of these successional stages. They are described below with a brief account of their value to tawny owls.

Establishment (Plate 2.5 upper). The early successional stage of both afforested and restocked crops consisting of newly planted crops up to 1 m top height (mean height of the 100 largest girthed trees per ha) and associated with the development of dense ground vegetation. Clear-felled areas are usually planted within 1-2 years. Small mammal populations increase with the amount of ground vegetation and tawny owls use these areas for hunting.

Pre-thicket (Plate 2.5 lower). Trees between 1 and 3 m top

Plate 2.5 Successional stages in a spruce forest. Establishment phase with trees less than 1 m high (upper) and pre-thicket phase with trees 1-3 m high (lower).

Plate 2.6 Successional stages in a spruce forest. Early-thicket stage (above), and late-thicket (below) with trees 3-10 m high. A very heavy cone crop is shown in the lower plate.

Plate 2.7 Successional stages in a spruce forest. Pole stage with trees above 10 m high (upper), and pole stage crop being clear-felled (lower).

height with ground vegetation at its most developed. These areas have the highest small mammal populations and are important foraging areas for tawny owls. The young trees provide perches from which the owls hunt.

Thicket (Plate 2.6). Trees between 3 and 10 m top height. Canopy closure results in the progressional loss of most ground vegetation. Variable tree growth and patches where trees die may result in sheltered glades. Most thicket crops are difficult to walk through. These areas are little used by tawny owls as small mammal populations are low and they are difficult or impossible to fly through.

Pole (Plate 2.7). Trees over 10 m until the time of clear-felling. Stands in sheltered situations may have a proportion of trees progressively removed (thinned) from the late-thicket stage onwards. Crops on more exposed sites often remain unthinned but may be susceptible to windthrow. Thinning and windthrow allow light to penetrate to the forest floor encouraging the re-establishment of some ground vegetation. Pole-stage crops provide the main roost and nest sites for tawny owls. Small mammal populations are low, but tawny owls may obtain some of their bird prey from these stands (Chapter 3).

There was a different distribution of these successional stages in each study area (Figure 2.10). During the course of the study in Kielder (1979-1991) thicket crops have declined while pole-stage crops have increased. Over the next 20 years there will be an increase in establishment and pre-thicket crops and a decrease particularly in pole-stage crops. In Glenbranter there has been little change during the course of the study (1984-1991), but over the next 20 years, the younger successional stage will decline while the older ones will increase.

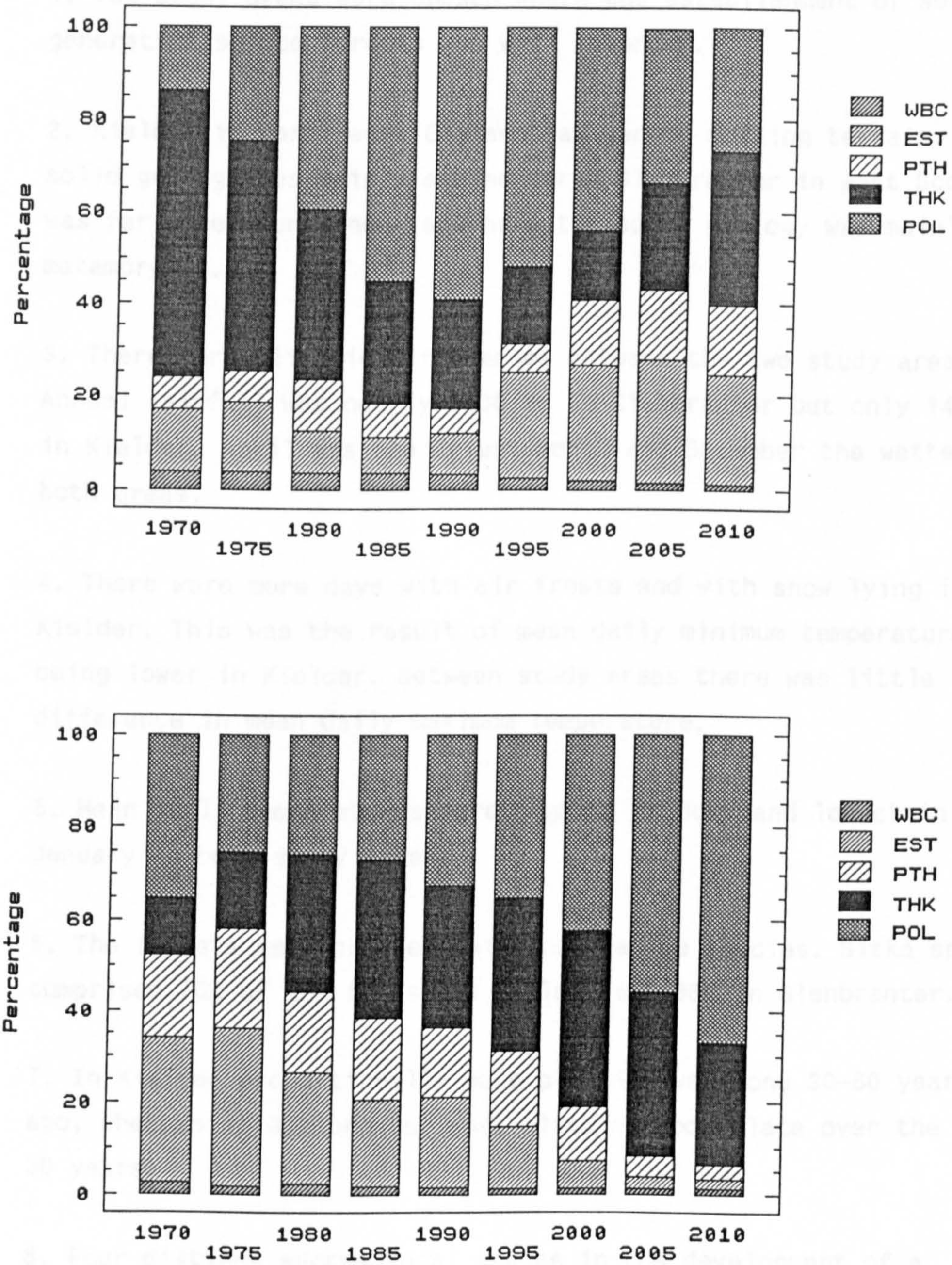


Figure 2.10 Predicted changes in distribution of successional stages as a percentage of the forest area in the Kielder (upper) and Glenbranter (lower) between 1970 and 2010 using the 1990 forest inventory database. WBC = windthrow and checked areas, EST = establishment, PTH = pre-thicket, THK = thicket, POL = pole.

2.5 Summary

1. Two study areas were chosen where the establishment of second-generation spruce forests was well advanced.

2. Kielder in north-east England had gently rolling terrain. The solid geology was mainly sedimentary. Glenbranter in west Scotland was far more mountainous and here the solid geology was mainly metamorphic.

3. There were climatic differences between the two study areas. Annual rainfall was nearly 2500 mm in Glenbranter but only 1400 mm in Kielder. April was the driest month and December the wettest in both areas.

4. There were more days with air frosts and with snow lying in Kielder. This was the result of mean daily minimum temperature being lower in Kielder. Between study areas there was little difference in mean daily maximum temperature.

5. Mean daily temperatures were highest in July and lowest in January in both study areas.

6. The forests were created using non-native species. Sitka spruce comprised 75% of the forest in Kielder and 88% in Glenbranter.

7. In Kielder proportionally more planting was done 30-60 years ago, whereas in Glenbranter most planting took place over the last 30 years.

8. Four distinct successional stages in the development of a plantation are described. These are establishment (trees less than 1 m high), pre-thicket (trees 1-3 m high), thicket (trees 3-10 m high) and pole (trees greater than 10 m). The importance of these stages for tawny owls is discussed.

9. The distribution of these four successional stages changed through time in each study area. The proportion of the pole-stage crops peaked in Kielder in 1990 and will peak in Glenbranter in 2010. The two younger successional stages (establishment and pre-thicket) will peak in Kielder around 2000-2005 but peaked in Glenbranter in 1975.

CHAPTER 3

FEEDING ECOLOGY

3.1 Introduction

Many mice and vole populations undergo cycles of abundance with peaks at three to five year intervals (Elton 1942; Finerty 1980; Hanski *et al.* 1991). Such dramatic changes in the availability of these rodents have led to the development of a range of hunting and reproductive strategies by their predators (Lack 1954; Lack 1966).

The tawny owl *Strix aluco* is capable of taking a wide range of prey but is particularly well adapted to take small mammals, breeding earlier and rearing larger broods in years when small mammals are abundant and refraining from breeding in years when they are scarce (Southern 1970).

To understand the feeding ecology of any predator, it is necessary to quantify what is eaten and what is available. Within the Kielder and Glenbranter study areas, field voles *Microtus agrestis* were the most important food of tawny owls (Petty 1987a; 1989; unpublished data). This rodent feeds largely on grasses, and is most abundant in ungrazed (by domestic animals) grassy habitats such as young conifer plantations and grassland (Hansson 1971; Corbet and Southern 1977; Charles 1981; Corbet and Harris 1991). It is less common in heavily grazed areas or in closed-canopy conifer forest with little ground vegetation (Charles 1981). Afforestation has ceased in both study areas, but clear-felling and replanting (restocking) commenced just over 20 years ago, and during the establishment and pre-thicket stages (2-12 years after felling) these grass-dominated areas provided suitable habitat for field voles (Chapter 2). Measurement of vole populations was therefore confined to restocked areas prior to canopy-closure. Vole abundance indices were then used to investigate the influence of food on various aspects of the population ecology of tawny owls (Chapters 4-8).

3.2 Methods

3.2.1 Food taken by tawny owls

Two methods were used to determine the diet of tawny owls.

A. Pellet analysis. Tawny owls do not have a crop, and small prey items such as voles, mice and shrews are usually swallowed whole. Larger items are often torn up into manageable pieces before being eaten. The undigested parts of prey are compressed in the stomach and egested orally as a pellet (Sturkie 1986; Duke *et al.* 1976).

Pellets were collected from below tree roosts. Each was placed in a polythene bag and labelled with the location, date collected and the estimated month when it was produced. The pellets were removed from the bags soon after collection, air dried, and then re-bagged for future analysis.

Pellets were analysed by carefully pulling them apart by hand under a dissecting microscope. Care was taken to examine all the matrix. Small mammals were identified from skulls and lower jaws and the number of individuals was calculated from which ever of these gave the highest score (Yalden 1977). The presence of birds was detected from grey powdered feather remains. The number and identity of birds could sometimes be determined from skulls, feet and undigested feathers identified from a reference collection. The humerus, if present, was measured using Vernier calipers and converted to body weight (Yalden 1977). Frog *Rana temporaria* remains were characteristic, often resulting in pellets composed entirely of bones. Skull and/or lower jaw bones of frogs were used to count the number of individuals. The presence of any invertebrate prey was recorded. Sandy/fibrous pellets were searched for the remains of chaetae from earthworms *Lumbricidae* (Southern 1970; Yalden and Warburton 1979; Yalden 1985).

The frequencies of prey items in pellets were converted to estimated biomass using mean weights for birds taken from Table 7 in Ratcliffe (1980) and for mammals from Corbet and Southern (1977).

Pellets do not give a totally accurate estimate of tawny owl diet. Lowe (1980) fed captive owls a range of prey which he recorded, and then analysed the pellets produced by the owls. The pellets gave a fairly accurate picture of what the owls ate. However, smaller prey were under-recorded, and he was able to produce seasonal correction factors for the three most commonly taken species (wood mouse *Apodemus sylvaticus*, bank vole *Clethrionomys glareolus* and field vole). Differences between summer and winter were apparently due to more efficient digestion in summer. Field voles were under-recorded least, with correction factors of 1.1 (winter) and 1.2 (summer), in contrast to correction factors of 1.2 (winter) and 1.6 (summer) for wood mice. These correction factors were not used in the present study because the aim was to produce only a broad assessment of the most important prey species.

A major drawback with pellet analysis is that outside the breeding season it is virtually impossible to get a large sample without a vast amount of effort. Tawny owls have large territories, and rarely re-use the same perch position, resulting in only one or two pellets being found at each location. Guérin (1932) and Uttendörfer (1939, cited in Southern 1954) state that pellets are cast before the birds roost, so pellets are rarely found at daytime roosts. Therefore, pellet collections were mainly restricted to the breeding season (March-July) when they were concentrated at roost/perch trees, usually within 50 m of the nest. Few pellets were collected from non-breeding pairs. More pellets were collected in the early part of the study compared with later, when the time-consuming capture of male owls became a more important priority.

B. Prey remains in nest sites

Prey items or their remains are rarely found in the nest during incubation. Whole or part-eaten prey are often present in nests from the start of hatching. Considerable caches can occur, with more than 10 whole prey items often being recorded, particularly in good vole years. Each part or whole prey item was identified, sexed

and weighed to the nearest 0.2 g (items <100 g) or 1 g (items >100 g). Female owls feed small pieces of prey to the chicks, always starting at the head and progressing to the tail of the prey, so it was always possible to sex part-eaten, small mammal prey from the genitals.

3.2.2 Measuring field vole abundance

Measurement of vole abundance was taken three times a year, in spring (March), summer (May/June) and autumn (September) so that relationships between clutch size (March-April), brood size (May-June) and overwinter mortality (September-March) in tawny owls could be investigated. Measurements were confined to restocked sites which had been planted between two and twelve years previously. In the time available it was not possible to estimate small mammal densities throughout the study areas (each was over 8000 ha). Therefore, a method was chosen to provide an index of small mammal abundance which comprised two elements:

A. Small mammal trapping. This intensive method was designed to provide data on changes in field vole abundance against which a quicker method was calibrated for extensive use in both study areas (see below). Data on the population structure of the small mammal community in the trapping areas were also obtained, together with a sample of field vole corpses to investigate their reproductive state and body condition (Hancock, Gurnell and Petty in press). It was similar to the small quadrat method described by Hansson (1975).

In 1984 one restocked site was randomly selected in each study area, from felled areas planted 2-5 years earlier. Each trapping area was 15 ha. In Kielder the site was replanted with Sitka spruce *Picea sitchensis* in 1979. The ground vegetation was dominated by the grasses *Deschampsia caespitosa* and *Molinia caerulea*, with rushes *Juncus* spp. abundant in the wetter areas. The Glenbranter site was similar, with Sitka spruce planted in 1983. The vegetation

comprised less *D. caespitosa*, but more *D. flexuosa*, *Agrostis* spp., *Festuca* spp. and bryophytes. In both trapping areas branches and stumps from the previous spruce crops were present in various stages of decay.

A 15 m x 15 m grid was superimposed on a map of each area. Twelve 15 m x 15 m squares were randomly selected at each assessment. Within a 1 m radius of the corner of each square, three break-back traps, modified to catch without bait (Plate 3.1) were set at the best location, usually across a vole run. The traps were adjusted to trigger when an object >5 g passed over the platform, such as juvenile field voles recently out of the nest.

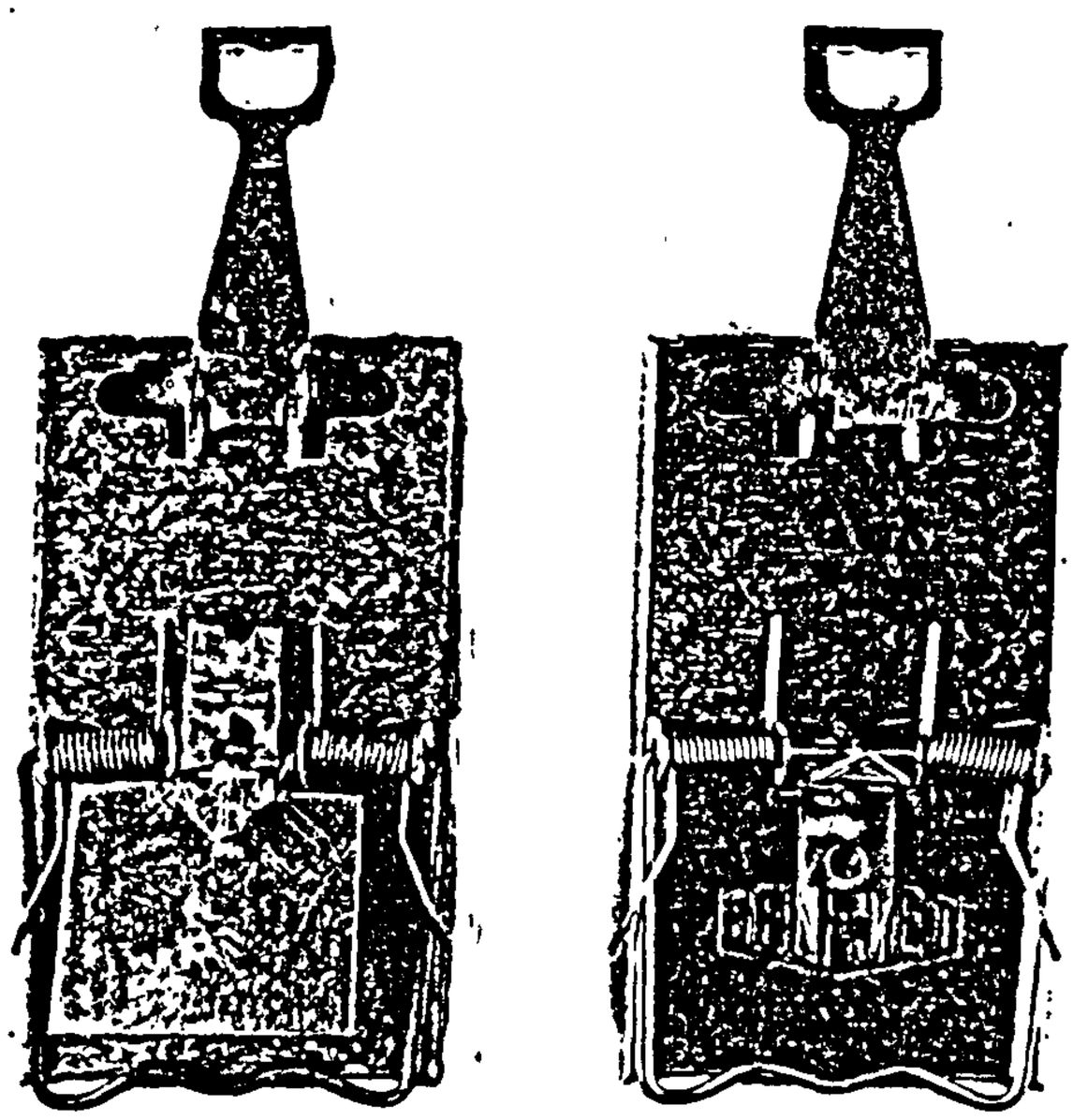


Plate 3.1 Break-back trap modified to catch without bait (left) and a trap without the modification. The modified trap is set at right-angles across a vole run, so that anything passing down the run has to cross the platform.

The 144 traps were set, then checked at 24 hourly intervals for 4 days making a total of 576 trap nights in each assessment. All the animals trapped were identified, and small mammals were labelled with the trap number and date caught and frozen for future analysis. The number of sprung (empty) traps was also recorded daily. Trap nights were adjusted when traps were occasionally lost during the trapping period or when fewer traps were set.

A field vole trapping index (VTI) was calculated as:

$$VTI = \frac{\text{field voles caught}}{\text{trap nights - traps sprung}} \times 100$$

and a shrew trapping index (STI) as:

$$STI = \frac{\text{common shrews + pygmy shrews caught}}{\text{trap nights - traps sprung}} \times 100$$

Removing sprung traps (empty) in the calculation of these indices was justified because, while there was a significant relationship in Kielder ($r_s=0.743$, $n=19$ $P<0.01$) and Glenbranter ($r_s=0.522$, $n=19$, $P<0.05$) between the number of traps sprung and total field voles caught, heavy rain, snow and hail also set off traps and it was impossible to separate these effects.

Break-back traps were used in preference to live-catch traps such as Longworths because:

A. They were far easier to carry over the rough ground on restocked sites.

B. They did not have to be baited, and were not biased towards catching species attracted to bait, such as wood mice and bank voles in Longworth traps.

C. They provided a sample of field vole carcasses to investigate reproductive condition and body size.

B. Vole sign indices (VSI). A quicker method of assessing vole abundance was adapted from Tapper (1979). Several restocked sites

were chosen in each study area (Figures 3.1 and 3.2). These were selected subjectively to give the widest possible coverage, with the object of detecting intra-and inter-year fluctuations in vole abundance over a much larger area than the trapping index. Tree growth on some VSI areas made them unsuitable for further assessment during the study. Replacement areas (newly planted) were then selected as near to the original area as possible. In each VSI area, 25 quadrats (25 cm x 25 cm) were searched for the presence (=1) or absence (=0) of each of the following vole signs.

Runways in the grass (RNI)
Fresh (not decomposing) vole droppings (FDI)
Old (decomposing) vole droppings (ODI)
Fresh (green) heaps of grass clippings (FCI)
Old (not green) heaps of grass clippings (OCI)

The scores for each of the above vole sign indices ranged from 0-25.

The relative abundance by area (to the nearest 10%) of plant species or species groups in each quadrat was also recorded. Species comprising <10% of the quadrat area were ignored.

The same restocked sites were used for each assessment and a similar route was followed each time. The position of each quadrat differed between assessments and was determined by walking 15-25 paces from the previous quadrat. A square metal frame of the quadrat dimensions was then thrown, and the assessment undertaken where it landed. One VSI assessment of 25 quadrats took about 20 minutes to complete.

To investigate which type or combination of vole sign indices calibrated best with the trapping index, one VSI assessment was undertaken in each trapping area. Data were available from 19 assessments carried out from June 1984 until June 1990 in Kielder. Only 13 were available from Glenbranter because six assessments were missed (autumn 1984, summer and autumn 1987, autumn 1988,

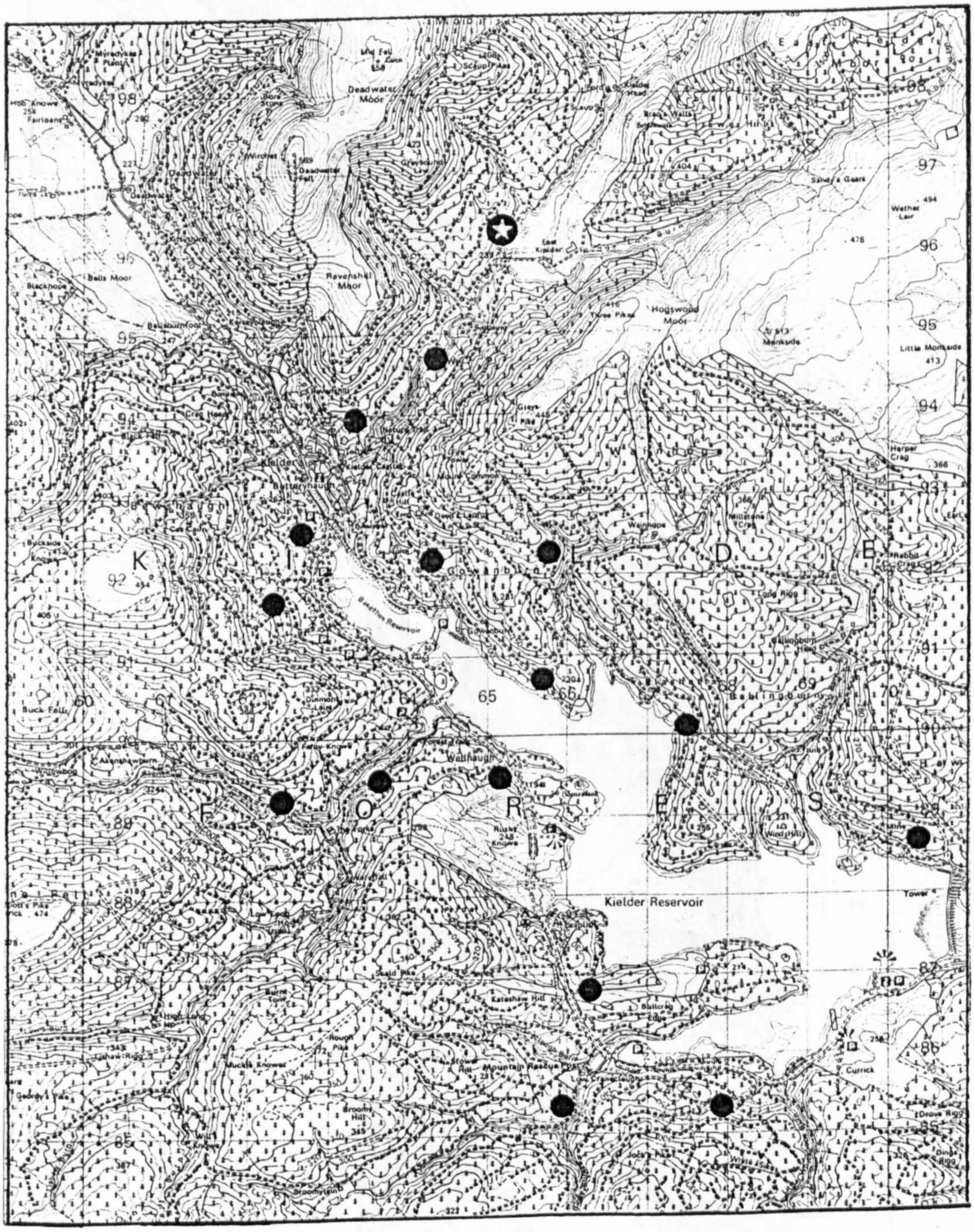


Figure 3.1 Location of the small mammal trapping area (circle and star) and vole sign indices areas (filled circles) in Kielder.

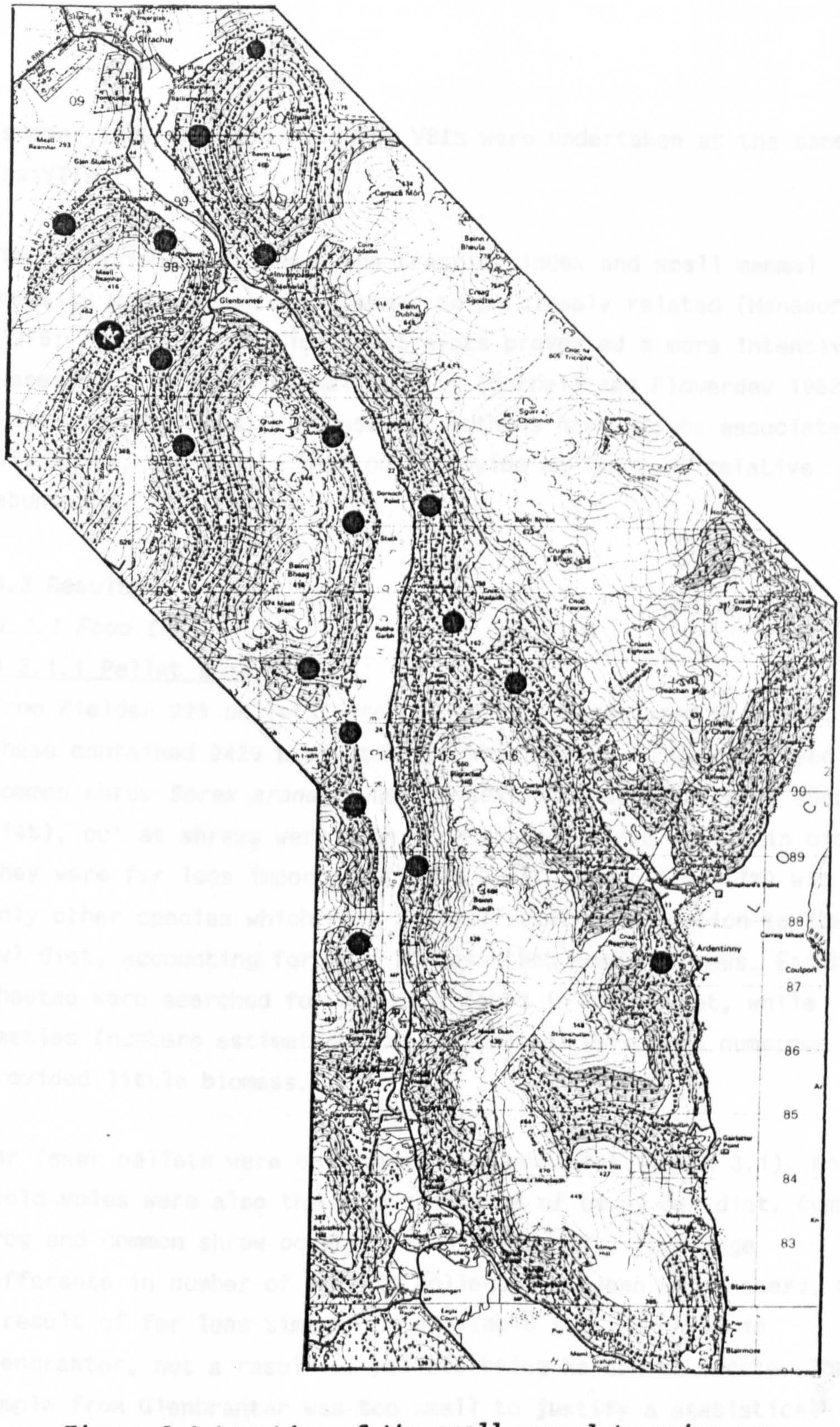


Figure 3.2 Location of the small mammal trapping area (circle and star) and vole sign indices areas (filled circles) in Glenbranter.

summer 1989 and summer 1990). VSIs were undertaken at the same time as VTIs.

The relationship between the trapping index and small mammal density was unknown but assumed to be closely related (Hansson 1975; Tapper 1979). Time constraints prevented a more intensive assessment of small mammal density (Gurnell and Flowerdew 1982). However, many density assessment methods have biases associated with them, and may in fact only provide an index of relative abundance.

3.3 Results

3.3.1 Food taken

3.3.1.1 Pellet analysis.

From Kielder 928 pellets were collected and analysed (Table 3.1). These contained 2429 prey items of which field voles comprised 72%. Common shrew *Sorex araneus* was the next most abundant prey species (14%), but as shrews were much lighter than field voles, in biomass they were far less important (Table 3.1). Common frog (7%) was the only other species which made a significant contribution to tawny owl diet, accounting for more biomass than common shrews. Earthworm chaetae were searched for but only found in one pellet, while beetles (numbers estimated from wing cases) were more numerous but provided little biomass.

Far fewer pellets were collected in Glenbranter (Table 3.1). Here field voles were also the main component of tawny owl diet. Common frog and common shrew occurred less frequently. The large difference in number of pellets collected between study areas, was a result of far less time being available for searching in Glenbranter, not a result of pellets being harder to locate. The sample from Glenbranter was too small to justify a statistical comparison of diet between study areas.

Table 3.1 Diet of tawny owls from Kielder (1980-1988) and Glenbranter (1983-1984) determined from 990 pellets.

Species	Wt g	Kielder		Glenbranter	
		No. (%)	Wt g(%)	No. (%)	Wt g(%)
Field vole	24.7	1757 (72.3)	43398 (78.1)	149 (94.3)	3680 (94.5)
Common shrew	9.4	347 (14.3)	3262 (5.9)	2 (1.3)	19 (0.5)
Bank vole	19.9	30 (1.2)	597 (1.1)	0 -	37 (0.9)
Wood mouse	18.4	16 (0.7)	294 (0.5)	2 (1.3)	-
Pygmy shrew	2.8	5 (0.2)	14 (0.0)	0 -	-
Mole	55.0	5 (0.2)	275 (0.5)	0 -	-
Rabbit	100.0	4 (0.2)	400 (0.7)	0 -	-
Total mammals		2164 (89.1)	48240 (86.8)	153 (96.9)	3736 (95.9)
Common frog	39.8	166 (6.8)	6607 (11.9)	4 (2.5)	159 (4.1)
Bird	50.0	13 (0.6)	650 (1.2)	0 -	-
Beetle	1.0	86 (3.5)	86 (0.1)	1 (0.6)	1 (0.0)
Total all prey		2429(100.0)	55583(100.0)	158(100.0)	3896(100.0)
Number of pellets		928		62	

Frog may also include some common toad.
Beetle = 58 Geotrupes spp., 1 Sylpha spp., 1 Dytiscus spp. and 26 unidentified.
Bird = 1 blackbird, 1 song thrush, 1 snipe, 1 green woodpecker, 1 meadow pipit, 1 tawny owl chick and 7 unidentified 15-20g birds.
Wt is estimated from the mean weight per prey item from Table 3.3

Table 3.2 Seasonal distribution of 2429 tawny owl prey items identified from 990 pellets collected in the Kielder study area (December 1980 - March 1988).

Species	Dec-Jan	Feb	March	April	May	June-July
Field vole	52(94.5)	42(84.0)	480(82.1)	560(75.5)	300(58.9)	323(66.2)
Common shrew	3(5.5)	4(8.0)	50(8.5)	77(10.4)	95(18.7)	118(24.2)
Other mammals	0 -	3(6.0)	16(2.8)	15(2.0)	13(2.6)	13(2.7)
Frog	0 -	0 -	34(5.8)	68(9.2)	50(9.8)	14(2.8)
Bird	0 -	1(2.0)	2(0.3)	4(0.5)	5(1.0)	1(0.2)
Beetle	0 -	0 -	3(0.5)	18(2.4)	46(9.0)	19(3.9)
Total	55(100.0)	50(100.0)	585(100.0)	742(100.0)	509(100.0)	488(100.0)
Number of pellets	14	16	220	285	203	190

Frog may also include some common toad.
There was a significant difference in the proportions of field vole, common shrew and frog in the six monthly/bimonthly periods (chi-squared =123.7, df=10, P<0.001)

The much larger sample of pellets at Kielder allowed seasonal trends in diet to be investigated (Table 3.2). No pellets were collected during August to November (inclusive). Field voles formed the highest proportion (95%) of tawny owl diet in mid-winter and then declined gradually, reaching their lowest incidence (59%) in May. This was offset by an increase in common shrew from 6% in December-January to 24% by June-July. Common frogs followed a similar trend but peaked earlier in April and May.

In Kielder, pellets were also collected during the breeding season from three other species of owls which bred in the study area (Figure 3.3). Compared to tawny owl, the proportion of field voles in the diet was about the same in short-eared owl *Asio flammeus*, less in barn owl *Tyto alba* and more in long-eared owl *Asio otus*. This difference was largely the result of barn owls taking more common shrews and long-eared owls taking fewer. Frog and beetle remains were only recorded in tawny owl pellets. Other mammals and birds formed very little of the diet of all four owls.

3.3.1.2 Analysis of prey in nests.

Over 1200 prey items were identified from nest sites in the two study areas (Table 3.3). More prey remains were recorded in Kielder (n=991) compared to Glenbranter (n=229), a result of a longer study period in Kielder and more prey items being recorded per nest visit.

The relative distribution of prey species was similar between study areas. Field voles were numerically the most abundant prey (Figure 3.4). Collectively birds formed the next most important group. The main differences between study areas were that fewer field voles and more bank voles and wood mice were taken in Glenbranter.

Converting the prey to biomass (Table 3.3 and Figure 3.4) demonstrated that birds were much more important in the prey delivered to nest sites than frequencies alone suggested. Birds

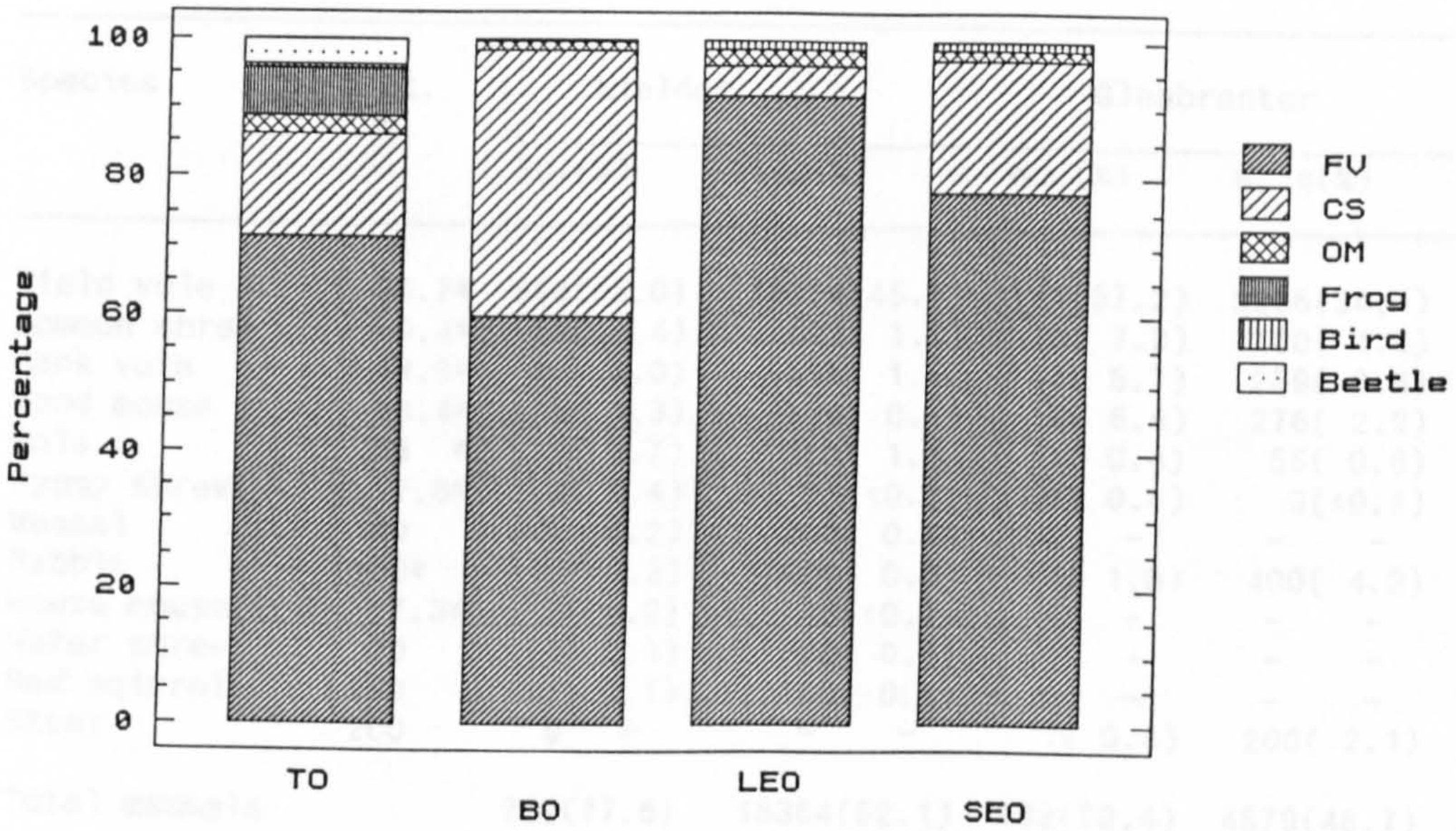


Figure 3.3 Diet (percentage frequency) of tawny owl (TO), barn owl (BO), long-eared owl (LEO) and short-eared owl (SEO) during the breeding season (March-July) determined from pellet analysis. Sample sizes of prey items are, tawny owl 2324, barn owl 976, long-eared owl 157 and short-eared owl 68. FV = field vole, CS = common shrew and OM = other mammals.

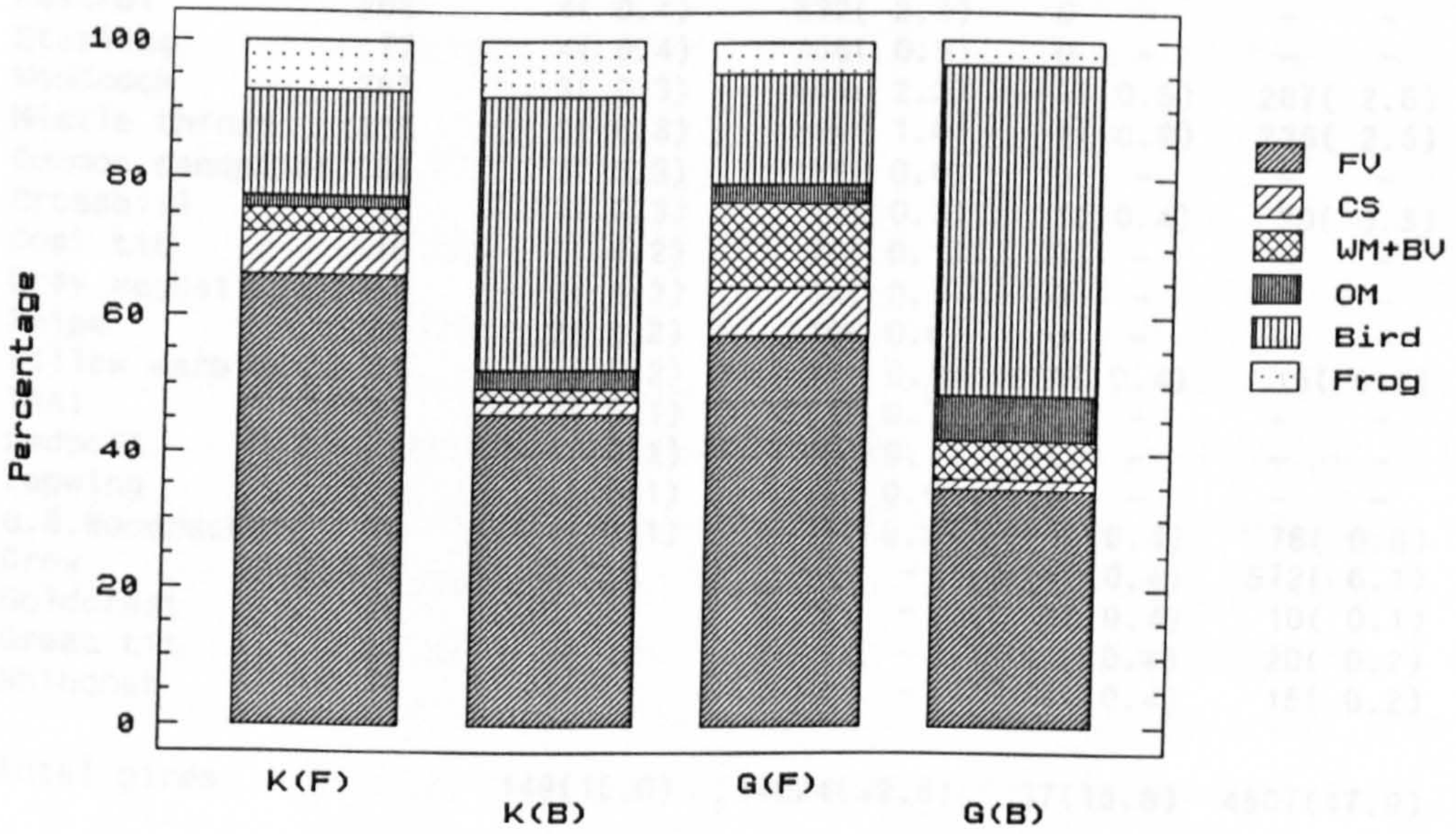


Figure 3.4 Prey items recorded from tawny owl nests in Kielder (K) and Glenbranter (G) in percentage frequency (F) and percentage biomass (B). FV= field vole, CS = common shrew, WM+BV = wood mouse and bank vole, OM = other mammals.

Table 3.3 Prey identified from tawny owl nests in Kielder (1979 - 1990) and Glenbranter (1983 - 1990).

Species	Wt. g	Kielder		Glenbranter	
		No.(%)	Wt.g(%)	No.(%)	Wt.g(%)
Field vole	24.7*	654(66.0)	16154(45.8)	131(57.2)	3236(34.4)
Common shrew	9.4*	63(6.4)	592(1.7)	16(7.0)	150(1.6)
Bank vole	19.9*	20(2.0)	398(1.1)	13(5.7)	259(2.8)
Wood mouse	18.4*	13(1.3)	239(0.7)	15(6.6)	276(2.9)
Mole	55 *	7(0.7)	385(1.1)	1(0.4)	55(0.6)
Pygmy shrew	2.8*	4(0.4)	11(<0.1)	1(0.4)	3(<0.1)
Weasel	100	2(0.2)	200(0.6)	0 -	- -
Rabbit	100*	2(0.2)	200(0.6)	4(1.8)	400(4.3)
House mouse	7.3*	2(0.2)	15(<0.1)	0 -	- -
Water shrew	20	1(0.1)	20(0.1)	0 -	- -
Red sqirrel	150	1(0.1)	150(0.4)	0 -	- -
Stoat	200	0 -	- -	1(0.4)	200(2.1)
Total mammals		769(77.6)	18364(52.1)	182(79.4)	4579(48.7)
Song thrush	80	43(4.3)	3440(9.8)	7(3.1)	560(6.0)
Chaffinch	22	15(1.5)	330(0.9)	7(3.1)	154(1.6)
Robin	19	13(1.3)	247(0.7)	1(0.4)	19(0.2)
Meadow pipit	20	11(1.1)	220(0.6)	3(1.3)	60(0.6)
Blackbird	92	8(0.8)	736(2.1)	3(1.3)	276(2.9)
Siskin	15	8(0.8)	144(0.4)	1(0.5)	15(0.2)
Tawny owl	50	8(0.8)	400(1.1)	0 -	- -
Woodpigeon	480	7(0.7)	3360(9.5)	1(0.5)	480(5.1)
Feral pigeon	425	4(0.4)	1700(4.8)	4(1.8)	1700(18.1)
Kestrel	208	4(0.4)	832(2.4)	0 -	- -
Starling	77	4(0.4)	308(0.9)	0 -	- -
Woodcock	267	3(0.3)	801(2.3)	1(0.5)	267(2.8)
Mistle thrush	118	3(0.3)	354(1.0)	2(0.9)	236(2.5)
Common sandpiper	66	3(0.3)	198(0.6)	0 -	- -
Crossbill	30	3(0.3)	90(0.3)	1(0.4)	30(0.3)
Coal tit	10	2(0.2)	20(0.1)	0 -	- -
Grey wagtail	17	2(0.2)	34(0.1)	0 -	- -
Snipe	106	2(0.2)	212(0.6)	0 -	- -
Willow warbler	15	2(0.2)	30(0.1)	1(0.4)	15(0.2)
Teal	261	1(0.1)	261(0.7)	0 -	- -
Redpoll	15	1(0.1)	15(<0.1)	0 -	- -
Lapwing	214	1(0.1)	214(0.6)	0 -	- -
G.S.Woodpecker	78	1(0.1)	78(0.2)	1(0.4)	78(0.8)
Crow	572	0 -	- -	1(0.4)	572(6.1)
Goldcrest	10	0 -	- -	1(0.4)	10(0.1)
Great tit	20	0 -	- -	1(0.4)	20(0.2)
Whinchat	15	0 -	- -	1(0.4)	15(0.2)
Total birds		149(15.0)	14024(39.8)	37(15.8)	4507(47.9)
Frog	39.8*	72(7.3)	2866(8.1)	8(3.5)	318(3.4)
Beetle	1.0	1(0.1)	1(<0.1)	2(0.9)	2(<0.1)
Grand total		991(100.0)	35255(100.0)	229(100.0)	9406(100.0)

*Weights for birds are from Ratcliffe (1980) and for mammals from Corbet and Southern (1977). * weights from whole prey items in owl nests in Kielder. Where part-grown juveniles accounted for most/all of a particular prey item (rabbit, tawny owl), then weights were reduced accordingly.*

composed a higher proportion of the overall biomass of prey than field voles in Glenbranter and a similar proportion to field voles in Kielder.

Prey items were found in nest sites from March to June inclusive. During this period there were substantial changes in the prey delivered to nests (Tables 3.4 and 3.5). A similar pattern was obvious in both study areas. Field vole frequencies were highest in March-April and lowest in May-June. Bird prey showed the opposite trend.

There were also annual changes in the relative occurrence of different prey species/groups in tawny owl nests (Tables 3.6 and 3.7). The amplitude of these changes was greatest in Kielder. For instance, the proportion of field voles in Kielder ranged from 17% (1989) to 85% (1987), compared to 32% (1989) to 85% (1983) in Glenbranter. Birds and frogs formed a higher proportion of food brought to nest sites in years when the incidence of field voles was low.

3.3.2 Food abundance

3.3.2.1 Small mammals caught in the trapping areas.

Trapping effort comprised over 21,000 trap nights. Field voles were by far the most abundant species caught in both study areas (Table 3.8). Common and pygmy shrews *Sorex minutus* were the next most abundant. Bank vole and wood mice were slightly more abundant in Glenbranter than Kielder resulting in a significant difference in the proportion of small mammals caught between study areas (Table 3.8). Surprisingly, a few water shrews *Neomys fodiens* were also caught. Few other animals were caught, with amphibians the most abundant.

There was a significant difference in the proportions of species trapped by season in both Kielder (chi-squared = 81.80, df=4, $P<0.001$, with pygmy shrew, water shrew, wood mouse and bank vole as

Table 3.4 Monthly distribution (percentage frequency) of 989 prey items from tawny owl nests in Kielder, 1979-1990.

Species group	March	April	May	June
Field vole	11 (84.6)	295 (80.6)	330 (61.0)	18 (26.1)
Common shrew	0 -	19 (5.2)	40 (7.4)	4 (5.8)
Bank vole	0 -	11 (3.0)	9 (1.7)	0 -
Wood mouse	0 -	8 (2.2)	4 (0.7)	1 (1.4)
Other mammals	0 -	2 (0.5)	16 (3.0)	0 -
Total mammals	11 (84.6)	335 (91.5)	399 (73.8)	23 (33.3)
Common frog	0 -	3 (0.8)	48 (8.9)	21 (30.5)
Bird	2 (15.4)	28 (7.7)	93 (17.2)	25 (36.2)
Beetle	0 -	0 -	1 (0.1)	0 -
Total prey	13(100.0)	366(100.0)	541(100.0)	69(100.0)

Table 3.5 Monthly distribution (percentage frequency) of 229 prey items from tawny owl nests in Glenbranter, 1983-1990.

Species group	March	April	May	June
Field vole	2(100.0)	33 (73.4)	85 (52.5)	11 (55.0)
Common shrew	0 -	2 (4.4)	14 (8.6)	0 -
Bank vole	0 -	3 (6.7)	10 (6.2)	0 -
Wood mouse	0 -	4 (8.9)	11 (6.8)	0 -
Other mammals	0 -	1 (2.2)	5 (3.1)	1 (5.0)
Total mammals	2(100.0)	43 (95.6)	125 (77.2)	12 (60.0)
Common frog	0 -	0 -	8 (4.9)	0 -
Bird	0 -	2 (4.4)	27 (16.7)	8 (40.0)
Beetle	0 -	0 -	2 (1.2)	0 -
Total prey	2(100.0)	45(100.0)	162(100.0)	20(100.0)

Table 3.6 Annual distribution (percentage frequency) of 989 prey items from tawny owl nests in Kielder, 1979-1990.

Species group	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
Field vole	25 (83.4)	42 (80.8)	78 (52.7)	56 (44.8)	5 (33.3)	77 (70.0)	50 (70.5)	5 (41.7)	198 (85.3)	73 (70.2)	4 (16.7)	43 (61.5)
Common shrew	1 (3.3)	1 (1.9)	11 (7.4)	10 (8.0)	0 -	10 (9.1)	2 (2.8)	1 (8.3)	10 (4.4)	8 (7.7)	1 (4.2)	8 (11.4)
Bank vole	2 (6.7	0 -	0 -	1 (0.8)	0 -	4 (3.7)	1 (1.4)	1 (8.3)	7 (3.0)	3 (2.8)	0 -	1 (1.4)
Wood mouse	0 -	1 (1.9)	2 (1.4)	0 -	0 -	2 (1.8)	0 -	0 -	4 (1.7)	1 (1.0)	0 -	3 (4.3)
Other mammals	1 (3.3)	2 (3.9)	4 (2.7)	8 (6.4)	0 -	1 (0.9)	1 (1.4)	0 -	1 (0.4)	1 (1.0)	0 -	0 -
Total mammals	29 (96.7)	46 (88.5)	95 (64.2)	75 (60.0)	5 (33.3)	94 (85.5)	54 (76.1)	7 (58.3)	218 (94.8)	86 (82.7)	5 (20.9)	55 (78.6)
Common frog	0 -	2 (3.8)	15 (10.1)	25 (20.0)	2 (13.3)	3 (2.7)	3 (4.2)	2 (16.7)	6 (2.6)	5 (4.8)	8 (33.3)	1 (1.4)
Bird	1 (3.3)	4 (7.7)	38 (25.7)	25 (20.0)	8 (53.4)	12 (10.9)	14 (19.7)	3 (25.0)	6 (2.6)	13 (12.5)	11 (45.8)	14 (20.0)
Beetle	0 -	0 -	0 -	0 -	0 -	1 (0.9)	0 -	0 -	0 -	0 -	0 -	0 -
Total prey	30(100.0)	52(100.0)	148(100.0)	125(100.0)	15(100.0)	110(100.0)	71(100.0)	12(100.0)	230(100.0)	104(100.0)	24(100.0)	70(100.0)

Table 3.7 Annual distribution (percentage frequency) of 229 prey items from tawny owl nests in Glenbranter, 1983-1990.

Species group	1983	1984	1985	1986	1987	1988	1989	1990
Field vole	11 (84.6)	16 (61.5)	6 (37.5)	26 (74.2)	19 (63.4)	17 (48.6)	6 (31.6)	30 (54.6)
Common shrew	0 -	0 -	0 -	0 -	1 (3.3)	8 (22.0)	5 (26.3)	2 (3.6)
Bank vole	0 -	1 (3.9)	1 (6.3)	1 (2.9)	3 (10.0)	1 (2.9)	0 -	6 (10.9)
Wood mouse	0 -	0 -	4 (25.0)	2 (5.7)	1 (3.3)	1 (2.8)	0 -	7 (12.7)
Other mammals	0 -	0 -	1 (6.2)	1 (2.9)	2 (6.7)	1 (2.8)	1 (5.3)	1 (1.8)
Total mammals	11 (84.6)	17 (65.4)	12 (75.0)	30 (85.7)	26 (86.7)	28 (80.0)	12 (63.2)	46 (83.6)
Common frog	0 -	4 (15.4)	2 (12.5)	0 -	0 -	1 (2.9)	1 (5.3)	0 -
Bird	2 (15.4)	3 (11.5)	2 (12.5)	5 (14.3)	4 (13.3)	6 (17.1)	6 (31.5)	9 (16.4)
Beetle	0 -	2 (7.7)	0 -	0 -	0 -	0 -	0 -	0 -
Total prey	13(100.0)	26(100.0)	16(100.0)	35(100.0)	30(100.0)	35(100.0)	19(100.0)	55(100.0)

Table 3.8 Summary of captures by study area for 19 trapping periods between summer 1984 - summer 1990.

Species caught	Kielder n (% Of A)	Glenbranter n (% of A)
Field vole	936 (82.2)	601 (75.5)
Bank vole	3 (0.3)	24 (3.0)
Wood mouse	4 (0.3)	20 (2.5)
Common shrew	170 (14.9)	133 (16.7)
Pygmy shrew	25 (2.2)	14 (1.8)
Water shrew	1 (0.1)	4 (0.5)
A. Total small mammals	1139 (100.0)	796 (100.0)
Other species		
Common frog	3 -	6 -
Common toad	8 -	4 -
Wren	0 -	4 -
Adder	1 -	0 -
Slug	2 -	5 -
B.Total trap nights	10658 -	10676 -

Comparing the proportions of different small mammals trapped in Kielder versus Glenbranter showed a significant difference (with bank vole, wood mouse and water shrew amalgamated into one category, chi-squared = 49.98, df=3, P<0.001; with the bank vole, wood mouse and water shrew category excluded, chi-squared = 2.68, df=2, NS)

Table 3.9 Seasonal distributions of small mammals caught in 19 trapping periods between summer 1984 and summer 1990 by study area.

Species	Spring (%)	Summer (%)	Autumn (%)
Kielder			
Field vole	209 (93.3)	351 (72.2)	376 (87.6)
Bank vole	0 (0.0)	1 (0.2)	2 (0.5)
Wood mouse	0 (0.0)	0 (0.0)	4 (0.9)
Common shrew	14 (6.3)	123 (25.3)	33 (7.7)
Pygmy shrew	1 (0.4)	10 (2.1)	14 (3.3)
Water shrew	0 (0.0)	1 (0.2)	0 (0.0)
Total Kielder	224 (100.0)	486 (100.0)	429 (100.0)
Glenbranter			
Field vole	156 (90.7)	206 (67.8)	239 (74.7)
Bank vole	4 (2.3)	12 (4.0)	8 (2.5)
Wood mouse	0 (0.0)	1 (0.3)	19 (5.9)
Common shrew	11 (6.4)	77 (25.3)	45 (14.1)
Pygmy shrew	1 (0.6)	8 (2.6)	5 (1.5)
Water shrew	0 (0.0)	0 (0.0)	4 (1.3)
Total Glenbranter	172 (100.0)	304 (100.0)	320 (100.0)

one category) and Glenbranter (chi-squared = 37.69, df=4, P<0.001, using the same categories as in Kielder) (Table 3.9). Field voles were the most abundant species caught in all seasons, but in spring they were relatively more abundant and in summer less abundant. These differences were caused largely by peak shrew numbers in the summer.

The proportion of species caught in the spring was not significantly different between study areas (chi-squared = 3.96, df=2, P>0.05, with water shrew, pygmy shrew, wood mouse and bank vole as one category), but there was a significant difference in summer (chi-squared = 15.51, df=3, P<0.01, with water shrew, bank vole and wood mouse as one category) and autumn (chi-squared = 38.47, df=3, P<0.001, with the same categories as in the summer). These differences were mainly the result of an increasing proportion of wood mice and bank voles caught in Glenbranter as the season advanced (Table 3.9). These species were both very scarce in the trapping area at Kielder.

3.3.2.2 Annual and seasonal changes of small mammals in the trapping areas.

The field vole population in Kielder fluctuated dramatically, with peak years in 1984, late 1986 extending into 1987, and the start of an increase in 1990, suggesting a three-year periodicity (Figure 3.5 upper). In Glenbranter, fluctuations in vole abundance were less dramatic, with less indication of a multi-annual cycle occurring. A slight peak in Glenbranter was evident in late 1986.

The vole populations in the two study areas were not synchronised. In 1984 the population was low in Glenbranter and high in Kielder. Autumn 1986 produced a peak in both populations, while in 1990 Kielder appeared to be increasing while Glenbranter was declining. This lack of synchrony was confirmed by correlation analysis (Figure 3.5 lower). If the populations were fluctuating together,

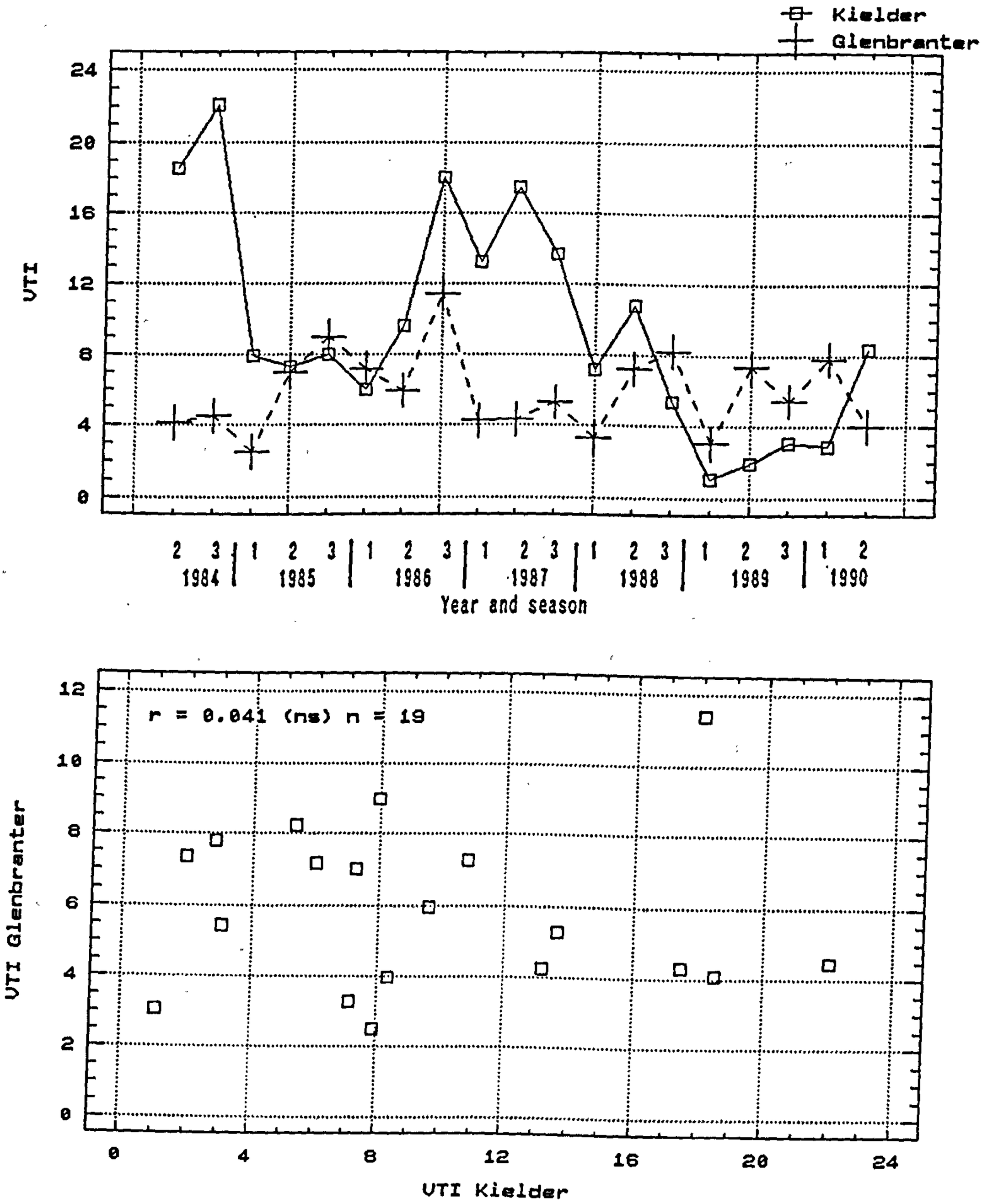


Figure 3.5 Vole trapping index (VTI) for both study areas from summer 1984 to summer 1990 (1=spring, 2=summer and 3=autumn) (upper), with a scatter plot showing the relationship between the seasonal indices from the two study areas (lower).

then the correlation coefficient (r) would be close to 1, while the actual value was near to zero.

In most years there was a seasonal increase of field voles from spring to autumn (Figure 3.5 upper). In the 10 complete study area/years available, increases between the spring and autumn assessments occurred in seven years, there was little change in two years (Kielder 1985 and 1987) and a decline in one year (Kielder 1988).

The relationship between the VTI (calculated from four days trapping) and an index calculated from the first two days of trapping, showed that the two-day index explained over 95% of the variation in the VTI when data from both study areas were combined (Figure 3.6). Pooling was justified as there was little difference in the regression lines between study areas. Therefore, if trapping is to be continued beyond this study, it would be advisable to limit this to two-days. As well as reducing the man hours involved, a two-day period reduces the risk of diminishing the small mammal populations through trapping.

There was no indication that shrew (common plus pygmy) populations fluctuated in synchrony with field vole populations in either study area (Figure 3.7), with less than 11% in the variability of the VTI explained by the STI (Figure 3.8).

3.3.2.3 Calibrating the vole trapping results with vole signs.

Correlation analysis was initially used to investigate the linear relationship between the VTI, a VTI calculated from two-days trapping and five vole sign indices (section 3.2.2) measured in both trapping areas. None of the vole sign indices could be classed as independent.

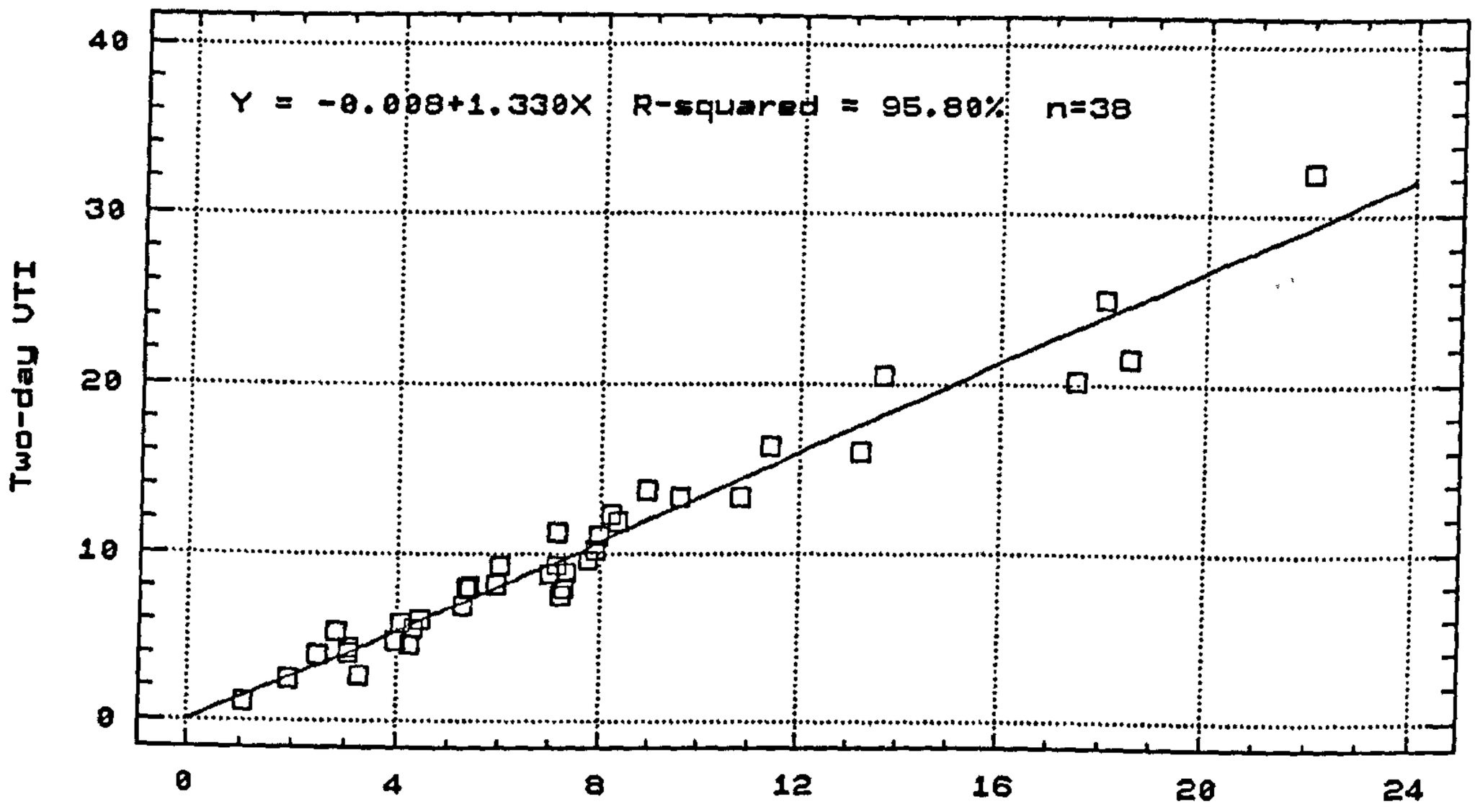


Figure 3.6 Relationship between the two-day VTI and four-day VTI. Each point represents one season.

Table 3.10 Coefficients of determination (r-squared) between two vole trapping indices and five vole sign indices from the two trapping areas (1984-1990) by season.

Independent variable	Dependent variable	Spring	Summer	Autumn	All seasons
Kielder		(n=6)	(n=7)	(n=6)	(n=19)
VTI	FDI	0.671	0.462	0.578	0.144
VTI2	FDI	0.689	0.460	0.631	0.157
VTI	ODI	0.681	0.638	0.486	0.262
VTI2	ODI	0.704	0.518	0.549	0.221
VTI	FCI	0.828	0.719	0.724	0.672
VTI2	FCI	0.867	0.681	0.745	0.711
VTI	OCI	0.506	0.222	0.092	0.084
VTI2	OCI	0.523	0.138	0.123	0.057
VTI	RNI	0.651	0.346	0.599	0.468
VTI2	RNI	0.808	0.241	0.605	0.420
Glenbranter		(n=6)	(n=4)	(n=4)	(n=14)
VTI	FDI	0.852	0.805	0.521	0.000
VTI2	FDI	0.771	0.289	0.578	0.004
VTI	ODI	0.558	0.611	0.780	0.003
VTI2	ODI	0.350	0.759	0.767	0.016
VTI	FCI	0.815	0.904	0.943	0.137
VTI2	FCI	0.709	0.817	0.956	0.007
VTI	OCI	0.490	0.342	0.005	0.001
VTI2	OCI	0.263	0.049	0.013	0.043
VTI	RNI	0.325	0.134	0.086	0.002
VTI2	RNI	0.142	0.039	0.133	0.004

VTI = vole trapping index *VTI2 = 2-day vole trapping index*
FDI = fresh droppings index *ODI = old droppings index*
FCI = Fresh clippings index *OCI = old clippings index*
RNI = vole run index

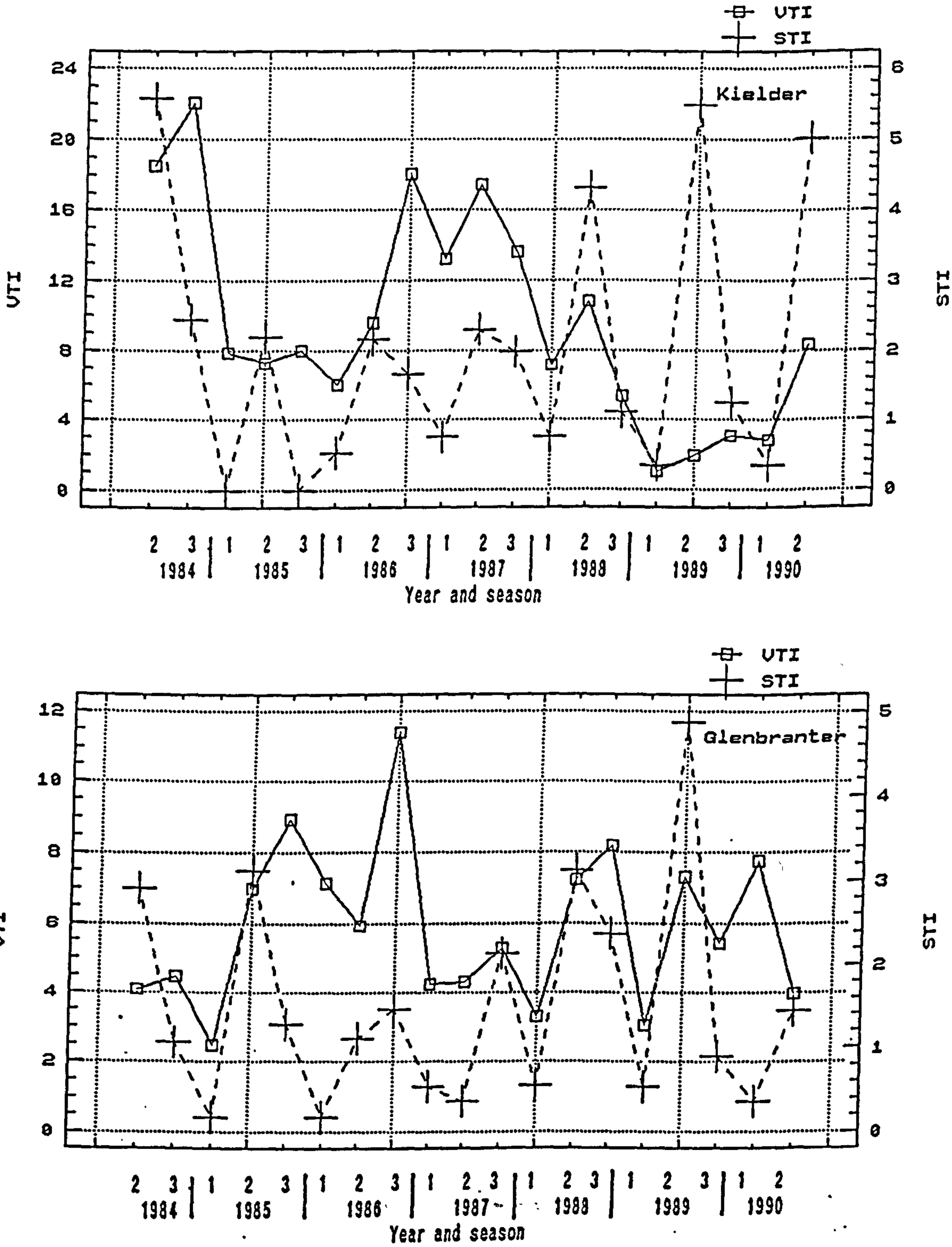


Figure 3.7 The vole trapping index (VTI) and shrew trapping index (STI) in Kielder (upper) and Glenbranter (lower) from 1984 to 1990 (1=spring, 2=summer and 3=autumn).

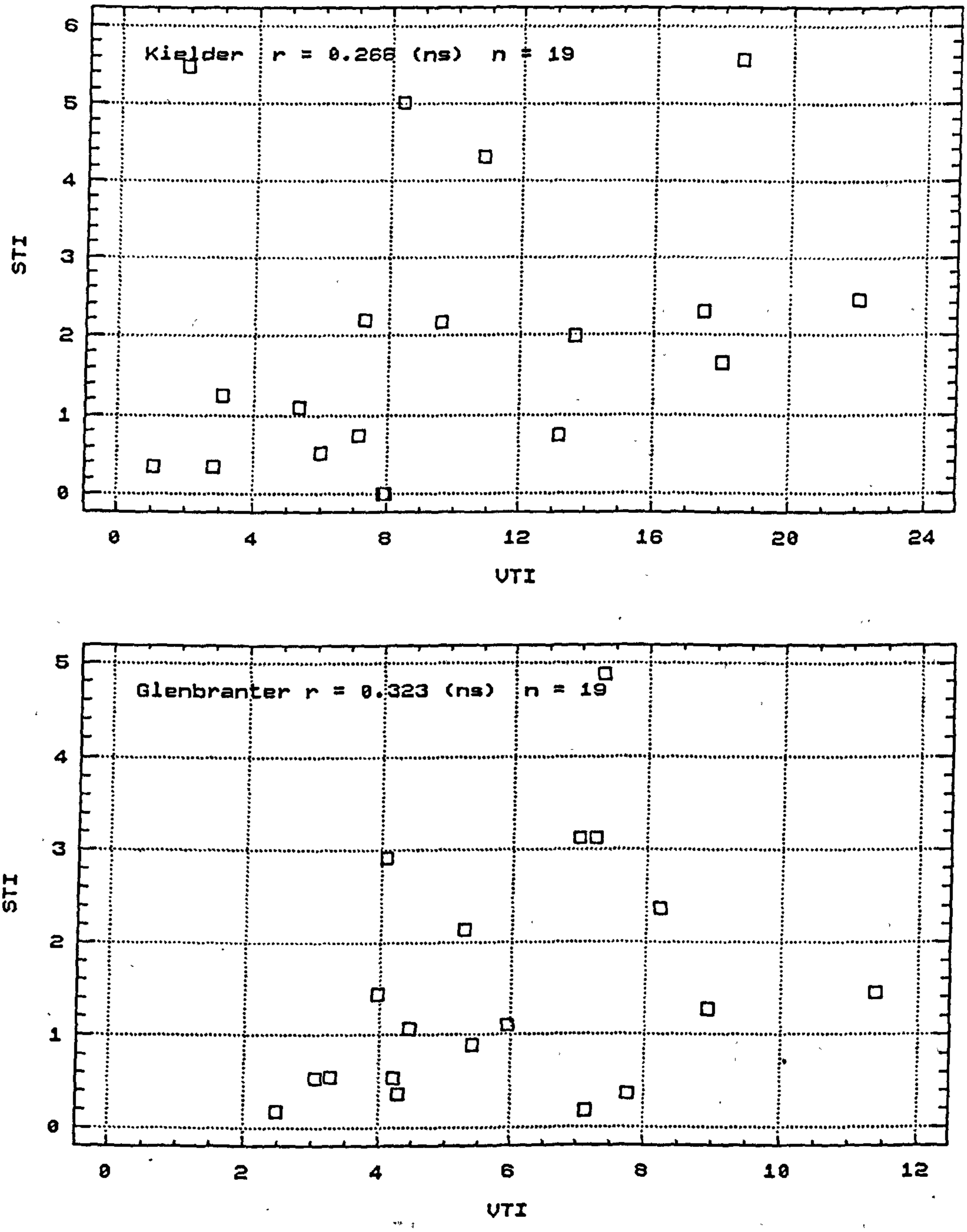


Figure 3.8 Relationships between the seasonal vole trapping indices (VTI) and shrew trapping indices (STI) for Kielder (upper) and Glenbranter (lower).

The fresh clippings index (FCI) consistently explained more of the variability with the VTI than any other index, and was the highest ranked index in five out of six season/study areas (Table 3.10). The exception was spring at Glenbranter, when the fresh droppings index (FDI) was ranked just above the FCI. When the seasonal FCIs were pooled by study area, considerably less of the variability was explained (Table 3.10). For Glenbranter the change was most dramatic, the seasonal indices individually explained between 82%-94% of the variation, but only 14% when pooled. This suggested there were strong seasonal influences and this was confirmed when the regression lines for VTI on FCI were plotted by season (Figure 3.9). The slope of these regressions changed seasonally, indicating more fresh clippings were present for the same vole density in spring than summer. For instance, a VTI of 10 would result in a mean of 19 vole sign quadrats with fresh clippings in spring at Glenbranter but only six in summer at Kielder (Figure 3.9). Presumably this was due to faster decay rates in summer, when clippings stayed greener for a shorter period, than in spring when temperatures are much cooler. The steeper slopes of the regression lines for Kielder compared to Glenbranter suggested that in Kielder clippings stayed greener for a shorter period.

The FCI quite accurately tracked the VTI compared to other indices, FDI for example (Figure 3.10). There was therefore little point in combining two or more indices, as then less of the variation with the VTI was explained.

Having identified FCI as the most highly correlated variable with VTI, the regression equations (Table 3.11) for VTI on FCI were then used to seasonally adjust the FCIs from all the vole sign index sites in each study area, to a predicted VTI score (PTI) (Table 3.12). The regressions of VTI on FCI for spring and summer at Glenbranter were very similar (Figure 3.9), so the data were pooled to give one equation (Table 3.11).

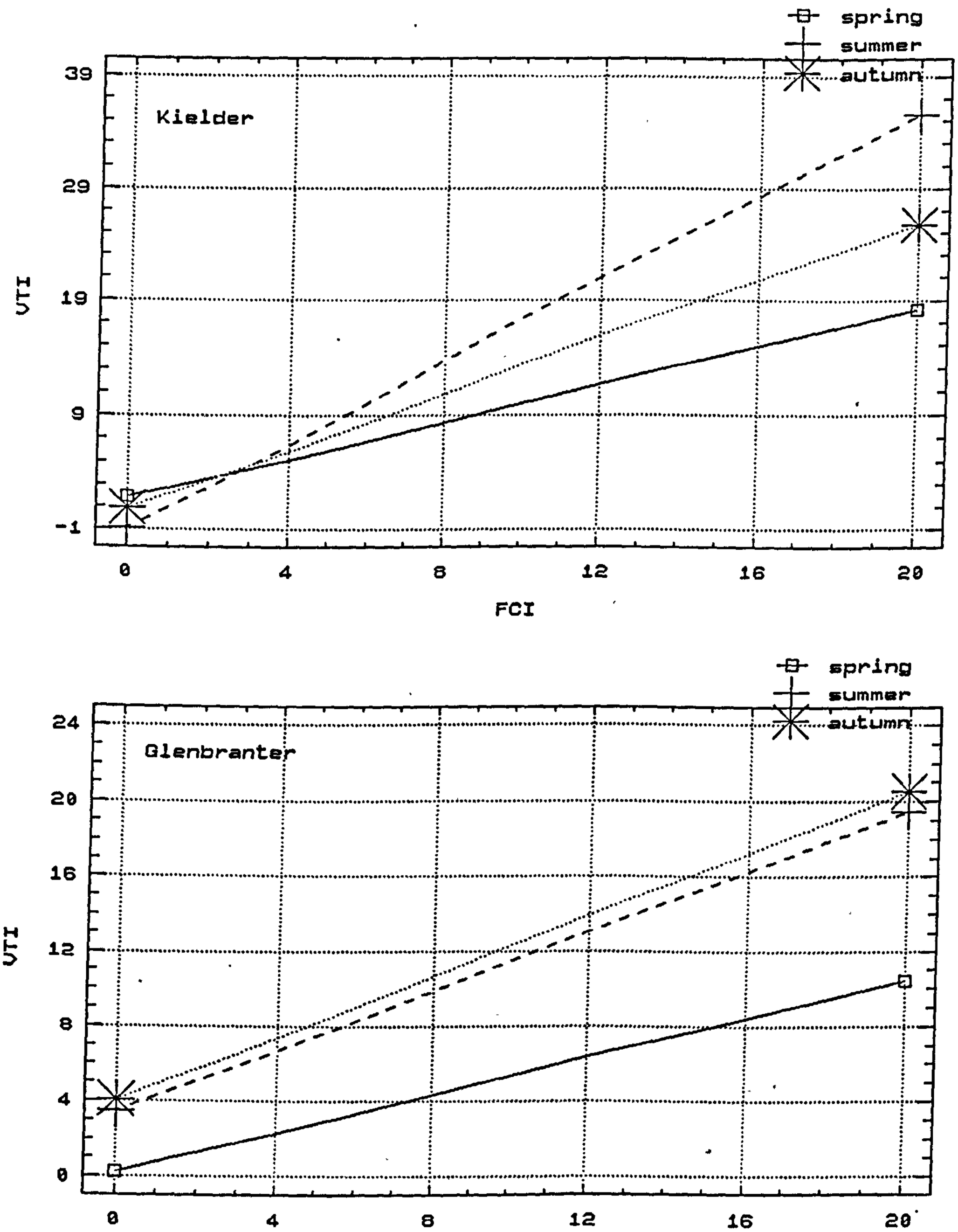
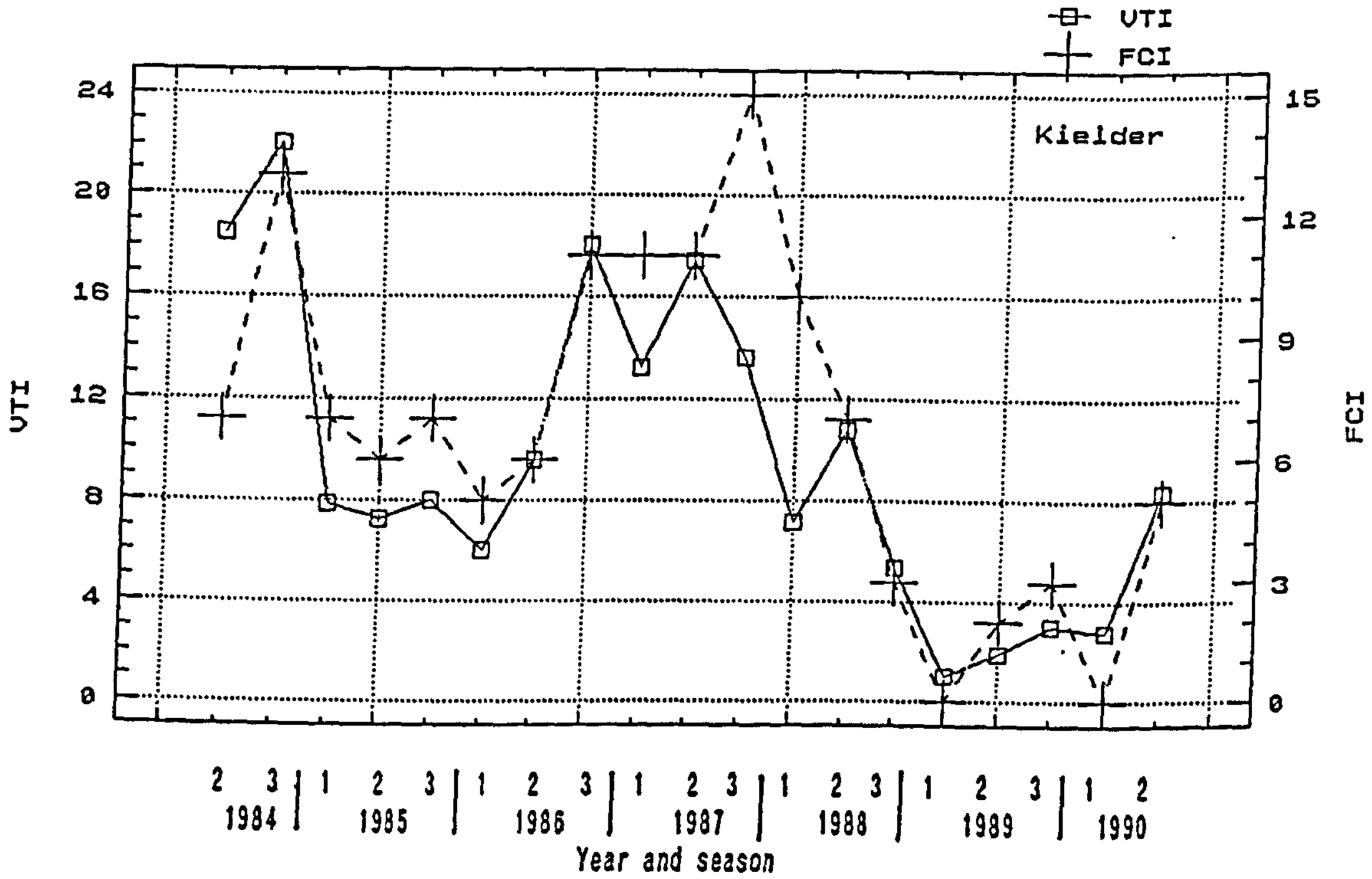


Figure 3.9 Regression lines for VTI on FCI by season for Kielder (upper) and Glenbranter (lower).



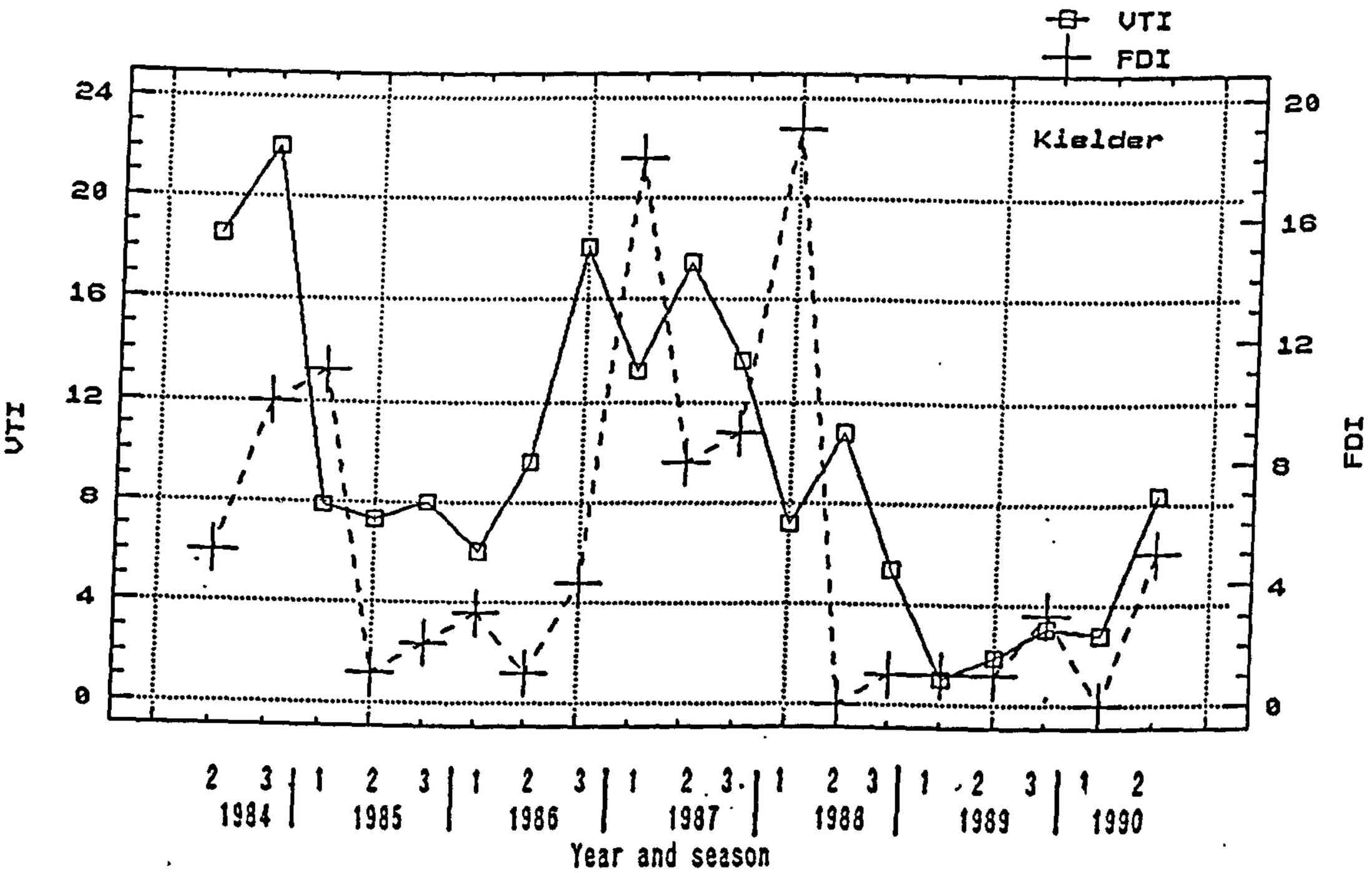


Figure 3.10 The relationship between the vole trapping index (VTI) and fresh clippings index (FCI) (upper) and fresh droppings index (FDI) (lower) in Kielder.

Table 3.11 Regression equations to convert the fresh clippings (FCI) (X) index to a predicted vole trapping index (PTI) (Y).

Study area	Season	Regression	n	r^2	rs	P
Kielder	spring	Y= 1.8783+0.8130X	6	0.828	0.928	0.038
Kielder	summer	Y=-0.9265+1.8290X	7	0.719	0.873	0.033
Kielder	autumn	Y= 0.9174+1.2424X	6	0.724	0.812	0.069
Glenbranter	spring	Y= 0.2540+0.5082X	6	0.815	0.943	0.035
Glenbranter	summer + autumn	Y= 3.6343+0.8452X	8	0.922	0.952	0.012

r^2= coefficient of determination; rs= Spearman Rank correlation coefficient

Table 3.12 Predicted vole trapping indices (PTI) by study area and season for any given FCI score (maximum range 0-25) using the regression equation in Table 3.11.

FCI	PTI				
	Kielder			Glenbranter	
	Spring	Summer	Autumn	Spring	Summer + autumn
0	1.878	-0.926	0.917	0.254	3.634
1	2.691	0.903	2.160	0.762	4.480
2	3.504	2.732	3.402	1.270	5.325
3	4.317	4.561	4.645	1.779	6.170
4	5.130	6.390	5.887	2.287	7.015
5	5.944	8.219	7.130	2.795	7.860
6	6.757	10.047	8.372	3.303	8.705
7	7.570	11.876	9.614	3.811	9.551
8	8.383	13.705	10.857	4.320	10.396
9	9.196	15.534	12.099	4.828	11.241
10	10.009	17.363	13.342	5.340	12.086
11	10.822	19.192	14.584	5.844	12.931
12	11.635	21.021	15.826	6.352	13.777
13	12.448	22.850	17.069	6.861	14.622
14	13.261	24.679	18.311	7.369	15.467
15	14.074	26.508	19.554	7.877	16.312
16	14.887	28.337	20.796	8.385	17.157
17	15.700	30.166	22.038	8.893	18.003
18	16.513	31.995	23.281	9.402	18.848
19	17.326	33.824	24.523	9.910	19.693
20	18.139	35.653	25.766	10.418	20.538
21	18.952	37.482	27.008	10.926	21.383
22	19.765	39.311	28.251	11.434	22.228
23	20.578	40.140	29.493	11.942	23.074
24	21.391	42.969	30.735	12.451	23.919
25	22.204	44.798	31.978	12.959	24.764

3.3.2.4 Trends in field vole abundance throughout both study areas.

The FCIs from each study area were corrected to PTIs (Table 3.13). Plotting the VTI against the mean PTIs in a time series by study area showed some interesting comparisons (Figure 3.11).

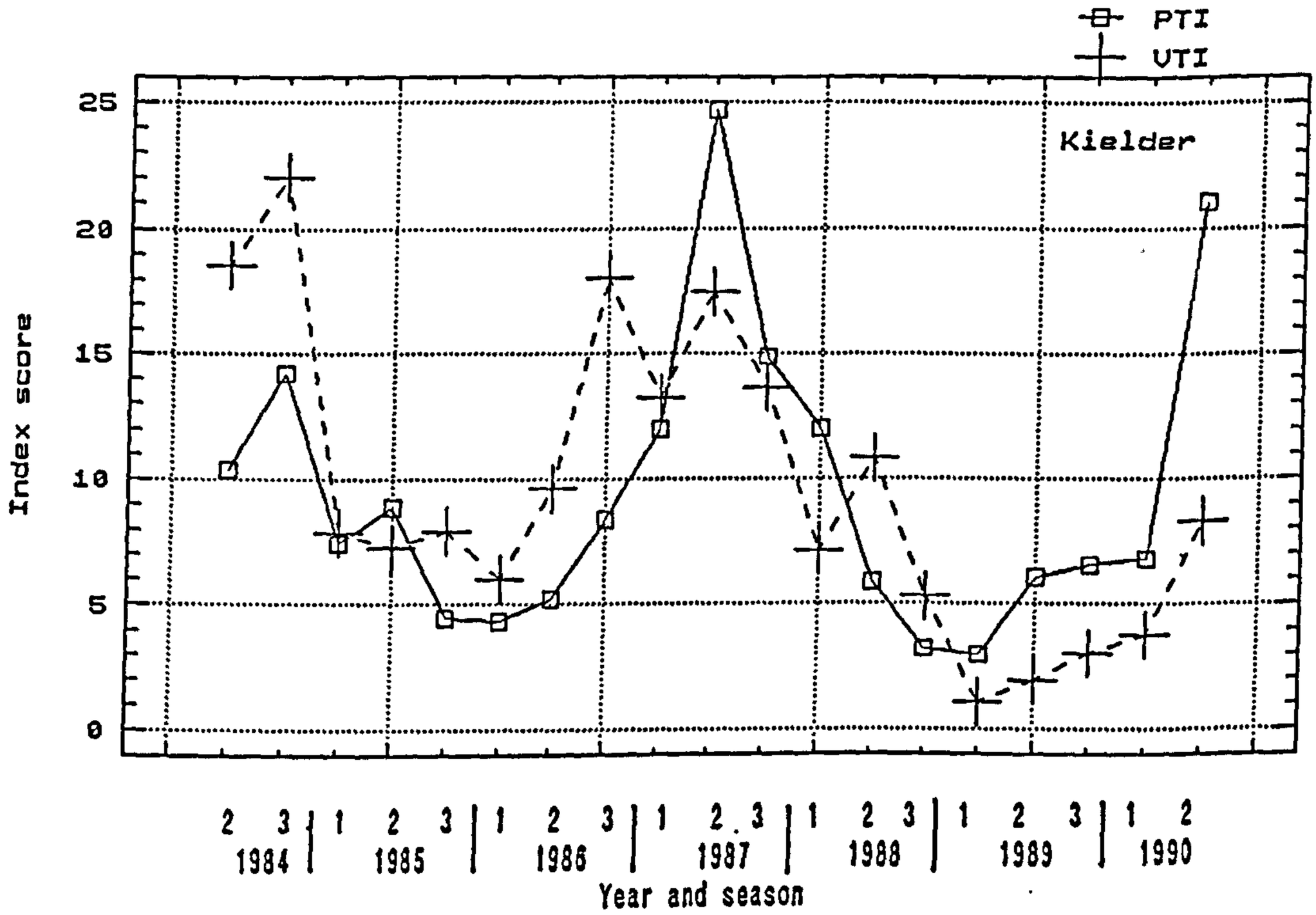
Trends in vole populations in the two trapping areas were similar to trends throughout each study area. However, in Kielder the peak in late 1984 in the trapping area appeared to be lower over the rest of the study area, while the peak in 1987 was higher than in the trapping area (Figure 3.11 upper). In summer 1990 the vole population in the trapping area lagged behind the main upward trend in Kielder. Both the VTI and the mean PTI suggest a three-year cycle in vole abundance.

It was less easy to determine whether multi-annual cycles in vole abundance occurred in Glenbranter (Figure 3.11 lower). To investigate this further a smoothing technique was used with the mean PTI scores. This enabled comparison between the two study areas to be made with seasonal effects reduced. The smoothed line (Figure 3.12) is the average of three points, the one against which it is plotted and the points on either side. This clearly showed the peak vole populations in Kielder in 1984, 1987 and 1990 (three-year intervals) and suggested a cycle of lower amplitude in Glenbranter with peaks in 1986 and 1990 (four-year interval) (Figure 3.12). How representative these Glenbranter data were of a longer time span was unknown, but other evidence in Kielder suggested that a three-year periodicity has occurred for at least four complete cycles with an additional peak in 1981 (Chapter 5).

In Kielder the variation in mean PTIs between low and high points in the vole cycle ranged from 3.01 (spring 1989) to 24.68 (summer 1987), compared to Glenbranter with a range of 1.43 (spring 1989) to 10.61 (autumn 1986) (Table 3.13). Over the entire period (summer 1984 to summer 1990) the mean PTI in Kielder was 9.45 (n=19, SD=5.89) and in Glenbranter 5.27 (n=13, SD=2.87). So vole

Table 3.13 Mean fresh clippings indices (FCIs) and the mean predicted VTIs (PTIs) (calculated using the regressions in Table 3.11) from each study area by season.

			FCI			PTI	
Year	Season	n	mean	SE	range	mean	SE
Kielder							
1984	summer	11	6.18	0.95	2-12	10.38	1.74
	autumn	14	10.71	1.11	4-19	14.23	1.38
1985	spring	13	6.77	0.86	2-12	7.43	0.71
	summer	14	5.36	1.38	0-16	8.87	2.53
	autumn	14	2.86	0.67	0- 7	4.47	0.83
1986	spring	14	3.07	0.82	0-12	4.38	0.67
	summer	14	3.36	0.86	0-11	5.21	1.60
	autumn	14	6.00	1.00	2-11	8.37	1.24
1987	spring	18	12.37	0.80	8-19	11.95	0.65
	summer	18	14.00	0.82	9-23	24.68	1.51
	autumn	18	11.28	1.05	3-19	14.90	1.30
1988	spring	18	12.39	0.90	4-19	11.95	0.73
	summer	18	3.72	0.83	0-12	5.88	1.52
	autumn	18	1.89	0.64	0-11	3.26	0.79
1989	spring	18	1.39	0.41	0- 7	3.01	0.34
	summer	18	3.83	0.89	0-14	6.09	1.63
	autumn	18	4.56	1.04	0-17	6.58	1.30
1990	spring	18	6.11	1.40	0-18	6.84	1.14
	summer	18	12.00	1.28	1-23	21.02	2.34
Glenbranter							
1984	summer	6	0.50	0.34	0- 2	4.06	0.29
	autumn	-	-	-	-	-	-
1985	spring	9	2.44	0.87	0- 7	1.50	0.44
	summer	10	4.90	1.11	1-13	7.78	0.94
	autumn	7	6.00	1.15	1-11	8.71	0.98
1986	spring	9	5.70	1.22	1-12	3.81	0.62
	summer	11	4.18	0.67	2- 8	7.17	0.57
	autumn	8	8.25	0.80	5-12	10.61	0.67
1987	spring	12	5.17	0.88	1-11	2.88	0.45
	summer	-	-	-	-	-	-
	autumn	-	-	-	-	-	-
1988	spring	13	5.92	1.32	0-14	3.26	0.67
	summer	13	1.62	0.40	0- 4	5.00	0.34
	autumn	-	-	-	-	-	-
1989	spring	13	2.31	0.67	0- 7	1.43	0.34
	summer	-	-	-	-	-	-
	autumn	13	5.00	1.04	0-10	7.86	0.88
1990	spring	13	8.23	1.35	1-16	4.44	0.69
	summer	-	-	-	-	-	-



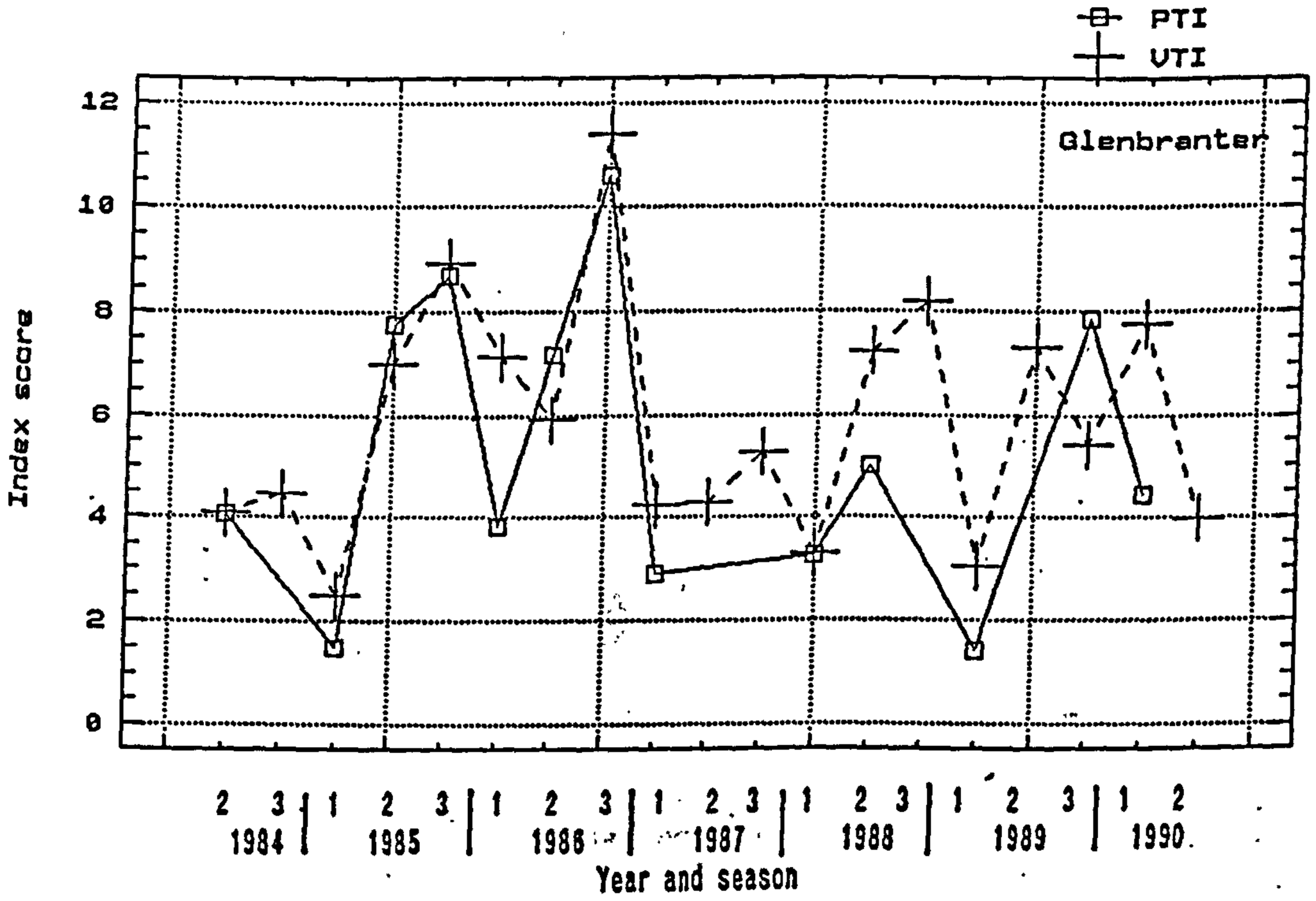


Figure 3.11 Vole population trends in the trapping area (VTI) and throughout each study area (PTI) in Kielder (upper) and Glenbranter (lower) from summer 1984 to summer 1990 (1=spring, 2=summer and 3=autumn).

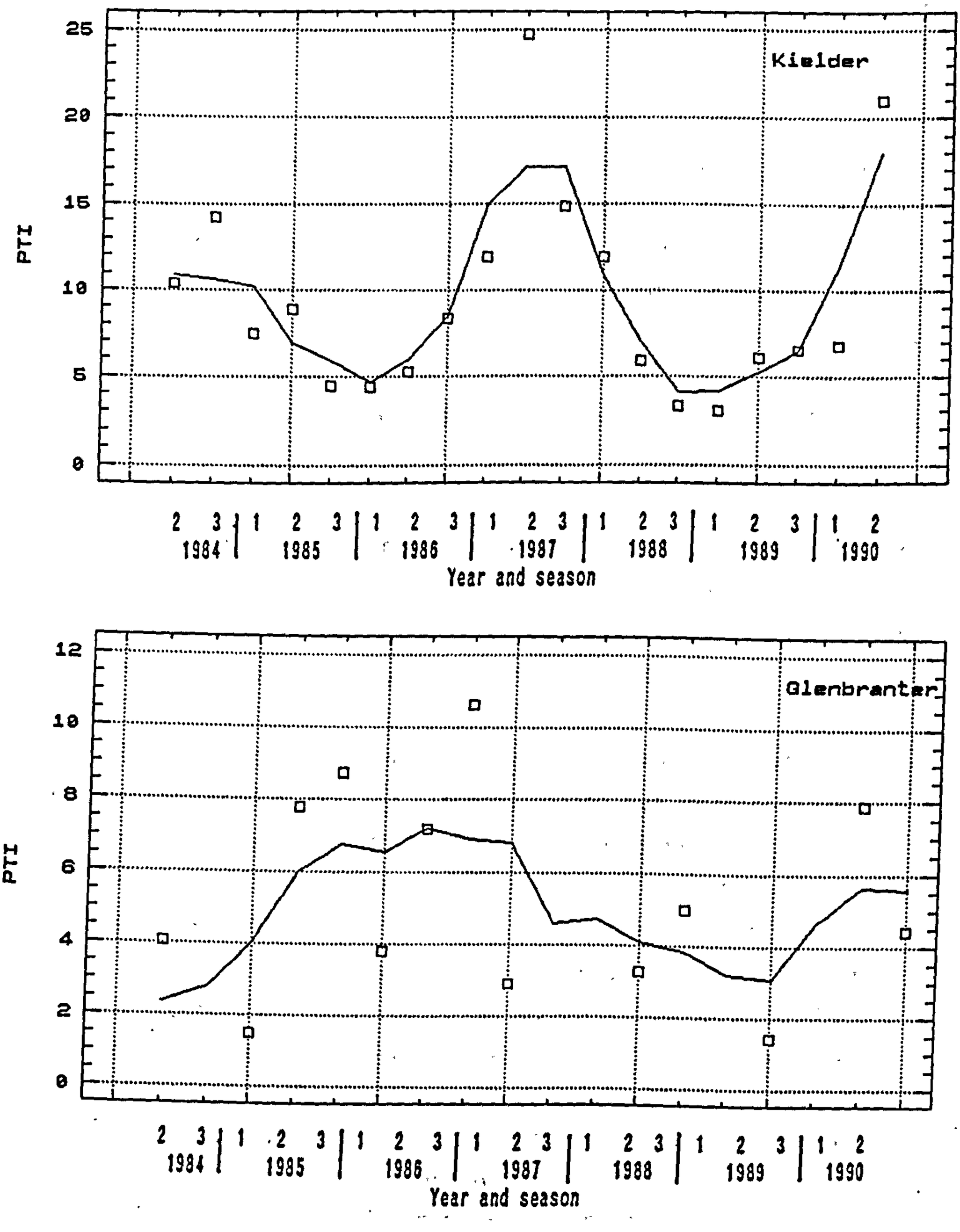


Figure 3.12 Smoothed seasonal PTIs for Kielder (above) and Glenbranter (below). The open squares are the actual mean PTI values (1=spring, 2=summer and 3=autumn).

populations were much higher in peak years in Kielder but lower in trough years in Glenbranter, with fluctuations at a higher overall level in Kielder.

Seasonal variations in vole abundance were investigated by comparing the residuals from the smoothed PTI lines and the actual PTI values (Figure 3.13). Seasonal effects were stronger in Glenbranter (ANOVA $F=25.10$, $df=2,10$, $P<0.001$) compared with Kielder (ANOVA $F=3.02$, $df=2,16$, $P=0.08$). These data suggest that variations in vole abundance were closely associated with the three-year cycle in Kielder, but in Glenbranter variations were more related to seasonal increases from spring to autumn (Figure 3.12).

In agreement with data from the trapping areas, vole population fluctuations throughout the two study areas were not synchronized as the correlation coefficient was near to zero when PTIs from Kielder were plotted against PTIs from Glenbranter (Figure 3.14).

In Kielder a further analysis investigated whether vole abundance was synchronized spatially. In fact there was considerable variation between some VSI areas. At each assessment there was a main trend with a few areas out of phase. This was particularly obvious when vole populations were low. At such times there were always some VSI areas where vole populations were out of phase with the main trend by a year either side. This can be shown by plotting histograms of the PTI scores by season throughout one complete vole cycle (1986-1988) (Figure 3.15). The modal PTIs were 5 or less when the vole population was low in spring 1986 and again by autumn 1988. During the peak from spring 1987 to spring 1988 the modal PTIs moved from just below 15 to nearly 25 then back to 15. However, when the PTIs were at their lowest (spring 1986 and autumn 1988), some areas had scores of 13-15, well into the range recorded in high vole years. These spatial variations in vole abundance can also be shown graphically (Figure 3.16) using the same three-years

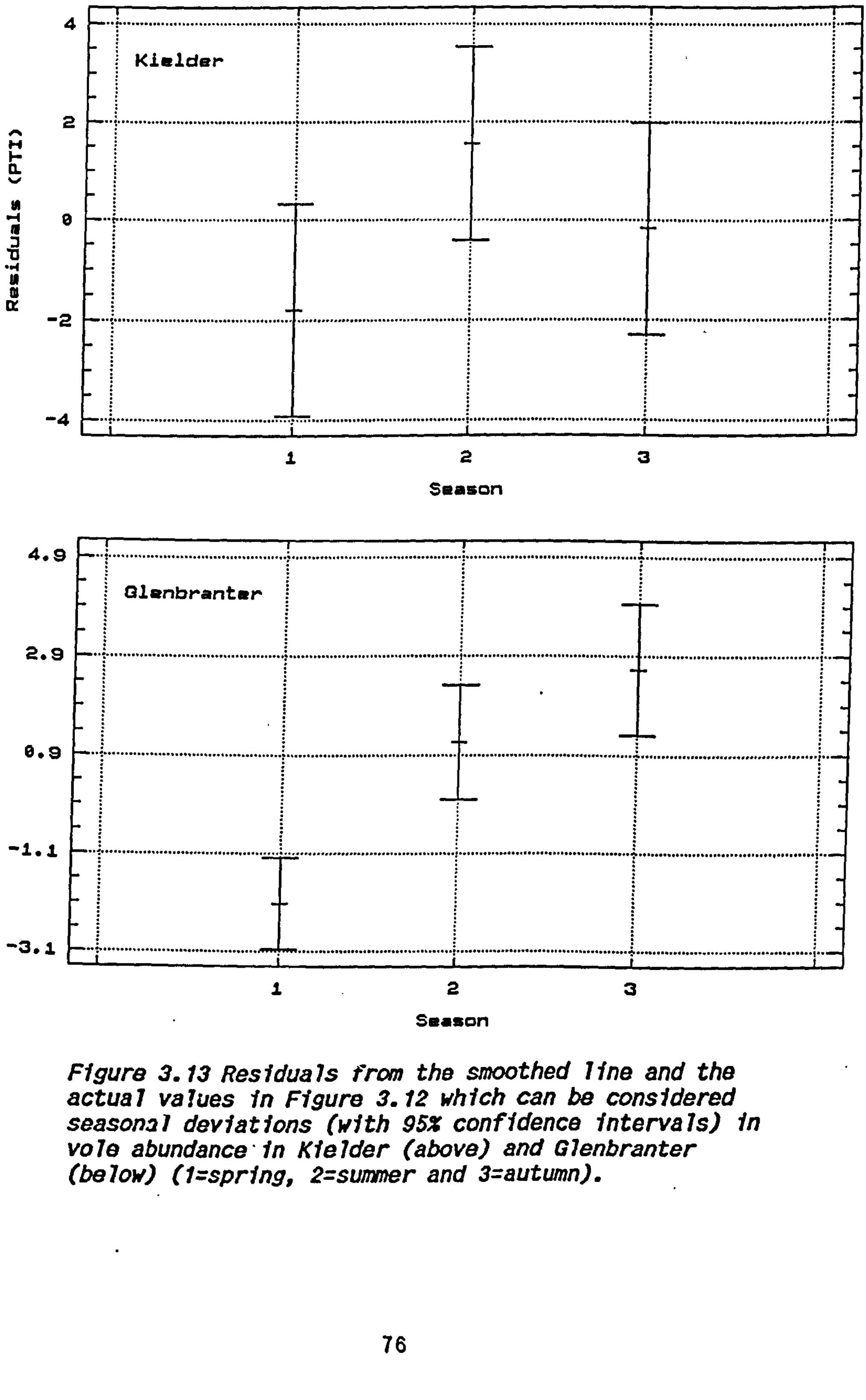


Figure 3.13 Residuals from the smoothed line and the actual values in Figure 3.12 which can be considered seasonal deviations (with 95% confidence intervals) in vole abundance in Kielder (above) and Glenbranter (below) (1=spring, 2=summer and 3=autumn).

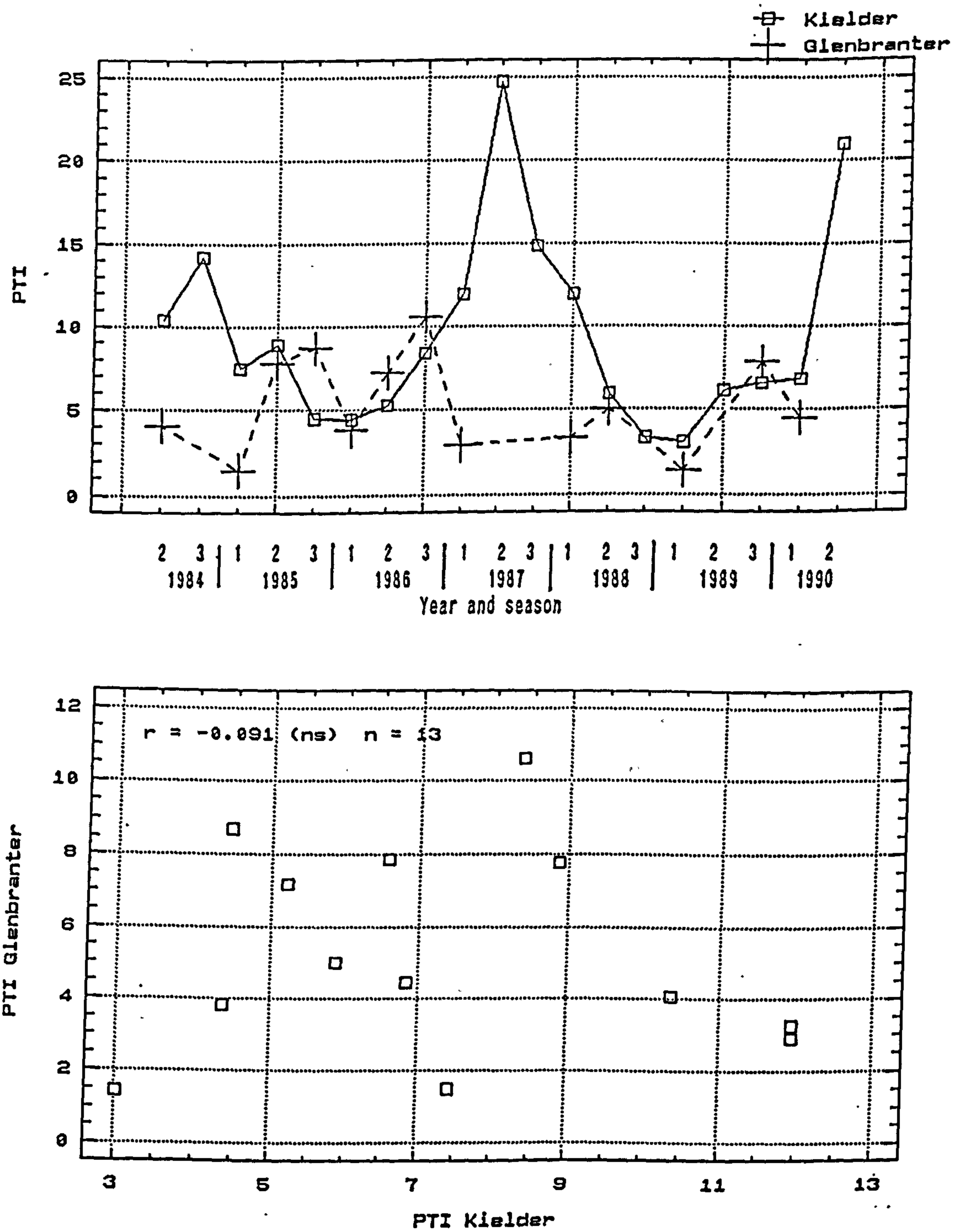
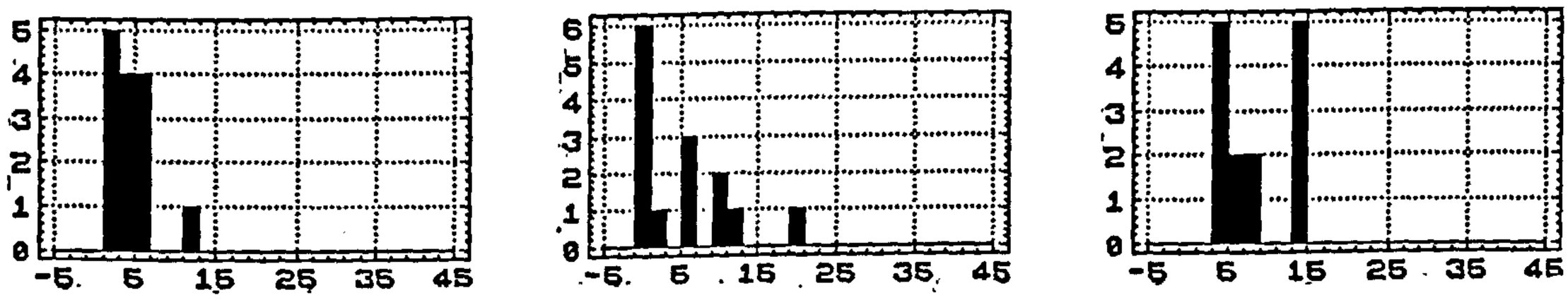


Figure 3.14 Mean PTIs for each study area from 1984 to 1990 (upper) with a scatter plot showing the lack of correlation between the two areas (lower).



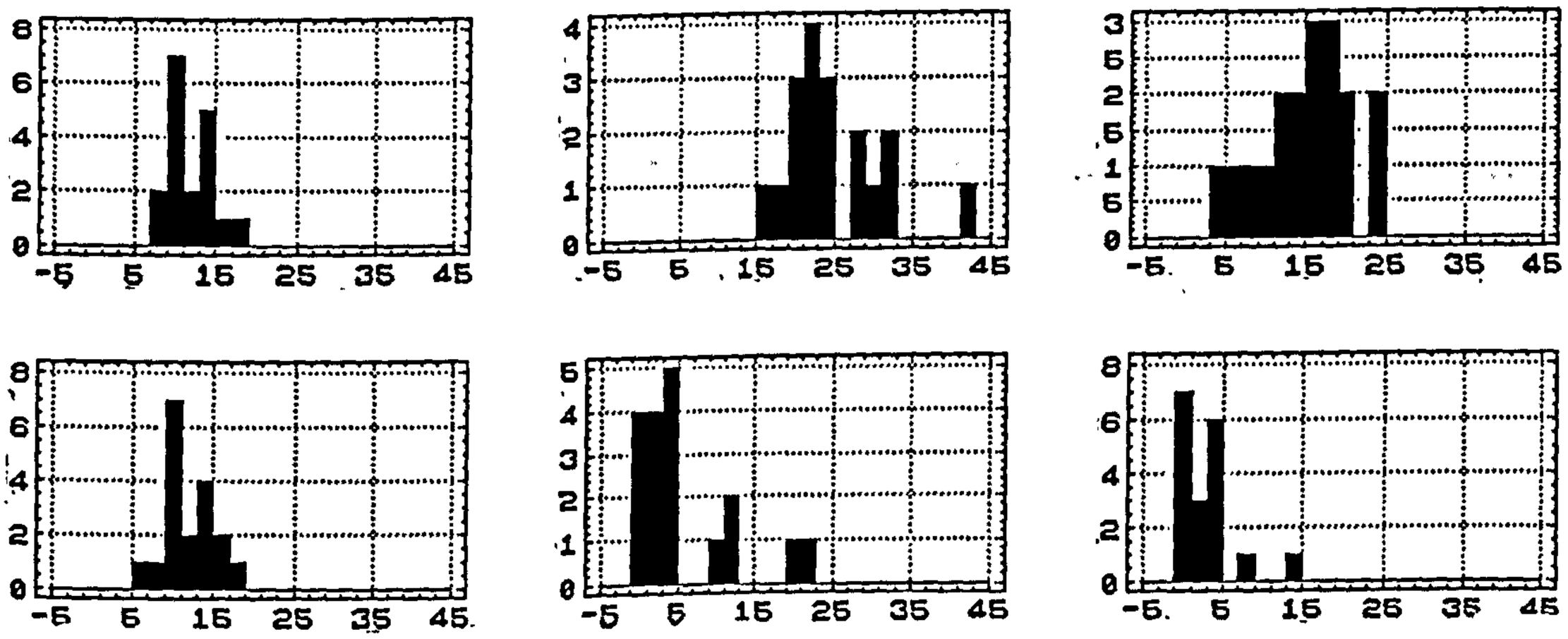


Figure 3.15 Histogram of PTI scores throughout one complete vole cycle in Kielder. The left-hand figures are for spring, the centre figures for summer and the right-hand figures for autumn. The upper row is for 1986, the middle 1987 and the lower 1988.

Figure 3.16 (next page) The maps predict vole abundance trends in suitable vole habitat throughout the Kielder study area using the PTI scores. No adjustments have been made for unsuitable vole habitat. The algorithm used to produce the maps was a modification of that described by Akima (1978). Kielder Water is in the centre and each square is 1X1 km. Predicted vole abundance values (PTIs) are, green <=4.4, yellow 4.5-7.4, orange 7.5-10.4, red 10.5-13.4, purple >=13.5.

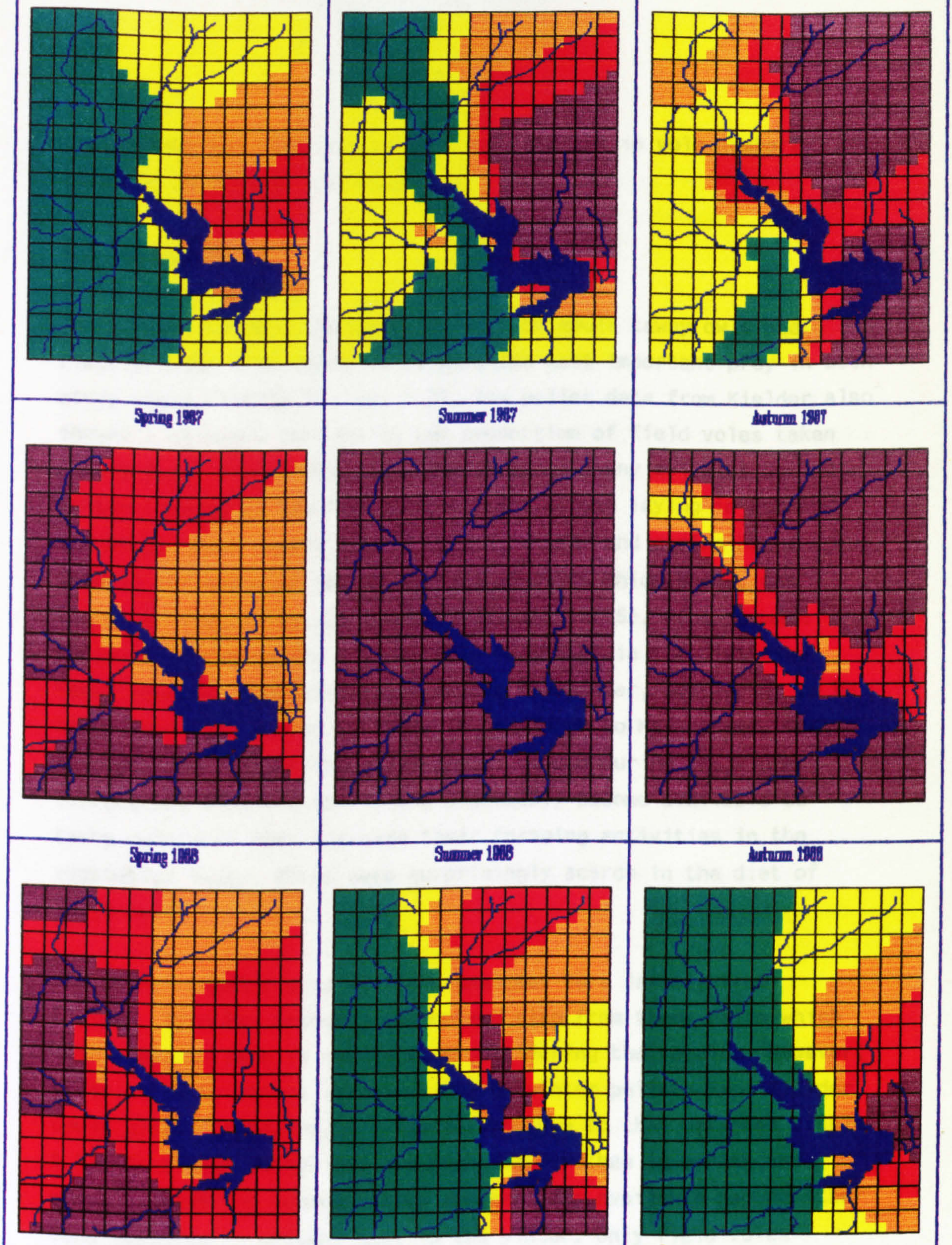


Figure 3.16 See caption on previous page.

(1986-1988) and strongly suggest that changes in vole numbers occurred in a wave-like manner.

3.4 Discussion

3.4.1 Tawny owl diet.

The pellet analysis reflects the diet of adult tawny owls and clearly shows that field voles were the most important prey in both study areas (Tables 3.1 and 3.2). The pellet data from Kielder also showed a seasonal decline in the proportion of field voles taken (Table 3.3). Field voles comprised most of tawny owl diet during winter through to the period just prior to egg laying in February and March. Food supply during autumn, winter and spring has a crucial influence on the proportion of pairs which breed, the timing of egg-laying and clutch size (Chapter 5). Frog, common shrew and birds became increasingly important in the diet from March onwards. Frogs hibernate during the winter, and appear to be taken when they emerge to spawn in the March to May period. Common shrews spend much of their time below ground during the winter (Corbet and Southern 1977), and presumably become available to tawny owls once they increase their foraging activities in the vegetation layer. Birds were surprisingly scarce in the diet of adult owls.

The pellet samples used in these analyses were largely from Kielder, from the breeding season and also from those pairs which laid eggs, so care is needed when considering the results. However, it is unlikely that a larger sample of winter pellets from Kielder would give a dramatically different picture to that obtained (Table 3.2). In winter, songbirds are much scarcer than in spring and summer, frogs and common shrews are far less available and no other food resource is present just in the winter. Only field voles provide a suitable winter food source, even in poor vole years.

In contrast to the pellet analysis, prey items found in the nest reflect what is fed to the chicks during April-June. Females attend

the chicks during this period, to brood and feed them, and do very little hunting themselves. They are also dependent on food provided by the male particularly during incubation and the early nestling period.

Prey items in nests showed a similar pattern in both study areas. Field voles comprised most of the items in March and then progressively declined in the following months (Tables 3.4 and 3.5). In contrast to their low incidence in pellets, birds formed a much larger proportion of the prey brought to nests, particularly in May and June.

These results differ from most other studies of tawny owl diet (from pellets) in woodlands in Britain. In lowland broadleaved woodland near Oxford, bank vole and wood mouse were the most abundant small mammals taken, with field voles occurring much less frequently (Southern 1954; Southern and Lowe 1968; Southern 1969; Southern and Lowe 1982; Hirons 1984). In Southern's study there was a seasonal shift in diet from predominantly small mammals in winter and early spring toward large mammals, such as moles *Talpa europaea* and juvenile rabbits *Oryctolagus cuniculus* in late spring and summer. Yalden's (1985) study in the Peak District with extensive moorland and patches of broadleaved woodland showed that tawny owl diet comprised largely birds (26% by weight), field voles (24%), earthworms (15%) and wood mice (10%). Interestingly the bird element was more important in the winter (32%) than the breeding season (22%). In small woods surrounded by farmland in Aberdeenshire, field voles and wood mice comprised 43% and 10% of the diet of tawny owls, with a shift towards more birds and larger mammals (moles and rabbits) and fewer small mammals from April through to May (Hardy 1977).

The diet of tawny owls in Kielder and Glenbranter fitted into the overall pattern of many studies although the species taken differed. Small mammals peaked in the winter to early spring diet,

and then declining as other prey, such as larger mammals and birds, became more available as the breeding season progressed (for reviews see Mikkola 1983 and Cramp 1985). Although searched for during pellet analysis, earthworm remains were only found in one pellet. This contrasts markedly with most other studies, where earthworms were a regular part of tawny owl diet (Yalden 1985). In both the Kielder and Glenbranter study areas this could be explained by the lack of heavily-grazed pastures for tawny owls to obtain earthworms and the prevalence of acid soils where earthworms are scarce or absent.

It was not possible to assess annual differences in the diet of tawny owls from pellet analysis in the present study because pellets were not collected in a consistent manner throughout the study. However, the food brought to nests was recorded in the same way from year to year and did show large annual differences in the relative abundance of the main prey species and a functional response by the owls to the availability of field voles. The proportion of field voles found in nests was closely related to the spring abundance of field voles throughout the study areas as measured by the mean spring PTIs scores (Figure 3.17). Around 80% of prey in nests were field voles when they were most abundant, but only about 20% in poor vole years.

Comparison of the diet (from pellet analysis) of the four species of owls in Kielder during the breeding season showed that all were heavily dependent on field voles (Figure 3.3). Long-eared owl, short-eared owl and barn owl were all relatively scarce in the study area compared to tawny owl. Long-eared and short-eared owl, the most highly specialized nomadic microtine predators (Chapter 1), were completely absent in low vole years, presumably because they moved out in response to declining vole numbers. Barn owls also disappeared during these low vole years, but probably due to mortality rather than movement (Anderson *et al.* 1989). In contrast, tawny owls stayed on territories, but many pairs did not breed

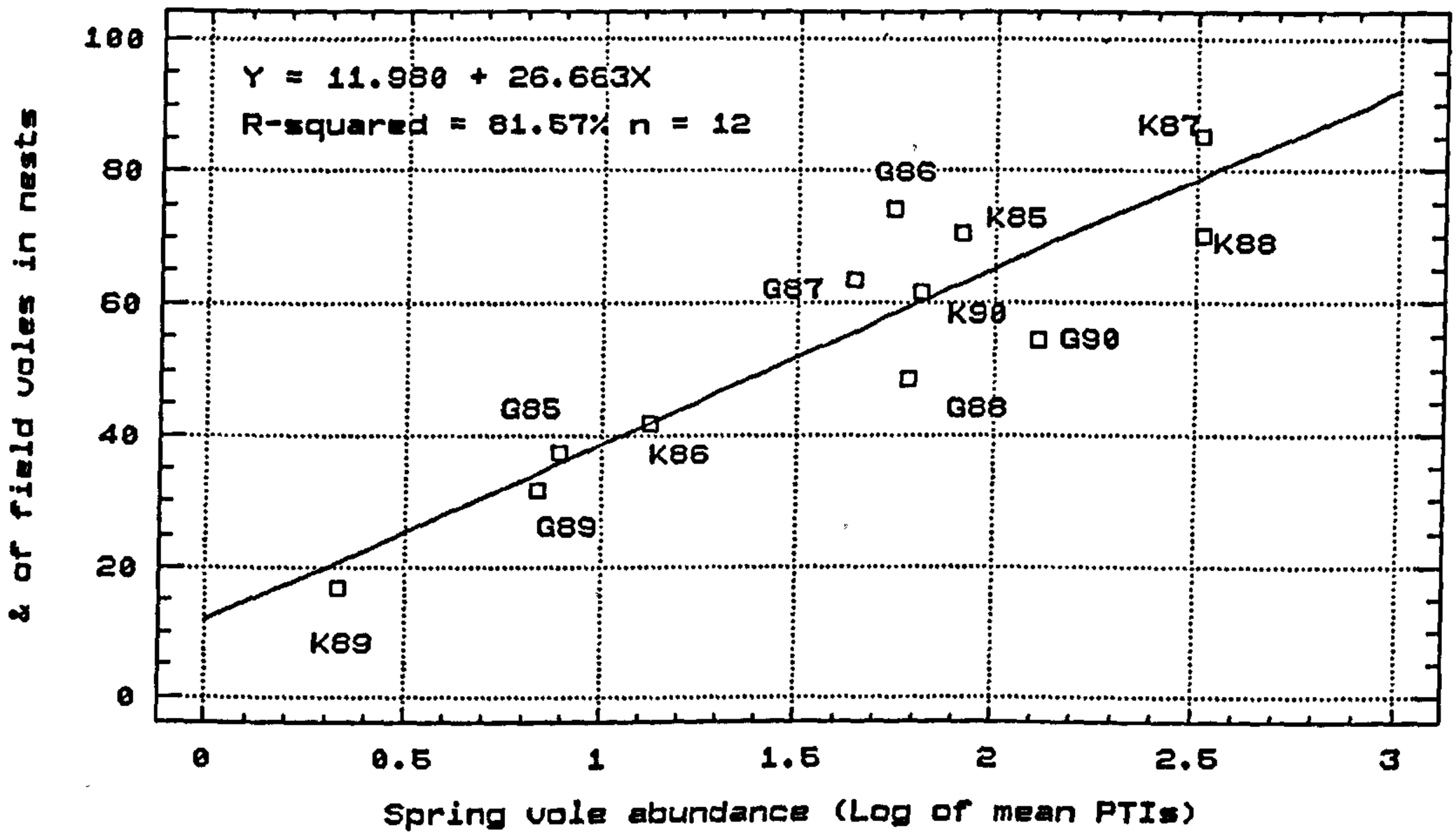


Figure 3.17 Relationship between annual spring vole abundance (log of mean PTIs) and the proportion of field voles in the prey delivered to tawny owl nests in both study areas from 1985-1990. This relationship was non-linear without transformation of the Y axis.

Table 3.14 The area of restocking in relation to plantation area in the two Forest Districts where the study areas were situated (data from Forestry Commission 1986; 1987; 1988; 1989).

Forest District		Year	Area under plantation (ha)	Area restocked (ha)
Kielder	*	85/86	51616	357
	*	86/87	51591	633
	*	87/88	50815	798
		88/89	50237	1016
Cowal	+	85/86	34250	242
	+	86/87	27021	393
		87/88	23521	223
		88/89	25168	220

** Includes both Borders and Kielder FD. Both had been amalgamated by 88/89*
+ Includes both Ardgartan and Cowal FDs. Part of Ardgartan was amalgamated into Cowal by 87/88

(Chapter 5) and adult mortality was higher (Chapter 6) when vole numbers crashed.

It is interesting to speculate whether the scarcity of long-eared owls, even in good vole years, was due to competition from the more powerful tawny owl or to a lack of the right habitat configuration. Other work on long-eared owl suggests that its ideal habitat consists of relatively small blocks of woodland surrounded by large open (vole rich) areas of grassland (including young plantation) (Village 1981; Marks 1986). As large blocks of even-aged plantations are gradually broken up into multi-aged stands through restructuring (Chapter 2), both study areas may become more attractive to long-eared owls in the future.

3.4.2 Prey availability

An earlier analysis had shown that field voles were an important part of the diet of tawny owls in Kielder (Petty 1987a). Therefore, attempts to measure prey abundance were directed towards quantifying population fluctuations of this species.

It was assumed that recently restocked areas were the main field vole habitat within both study areas. Clear-felled and replanted areas were quickly colonized by vegetation, which was usually complete within two to four years from felling apart from some areas with rows of branches left from the previous crop. In North America, a review of 21 studies revealed a significant increase in small mammal abundance and diversity following clear-felling (Kirkland 1990).

In both Kielder and Glenbranter, grasses were initially the dominant vegetation group on restocked sites. These comprised largely *Deschampsia caespitosa*, *D. flexuosa*, *Molinia caerulea*, *Agrostis* spp. and *Poa* spp. Other major components of the vegetation were *Juncus* spp., *Carex* spp. and bryophytes. Roe deer *Capreolus capreolus* selectively browsed regenerating broadleaved trees,

shrubs and herbs and effectively prevented these becoming part of the vegetation, thus allowing monocotyledons to predominate (Suida *et al.* 1969; Hosey 1974; Hinge 1986).

Canopy closure occurs 15-20 years after planting when much of the grassy vegetation is shaded out. Thicket and pole-stage stands were therefore assumed to provide a much poorer habitat for field voles. Charles (1981) recorded an average vole density of 5 per ha in closed-canopy spruce forests (>20 years old) in south Scotland, and noted that voles were probably absent from some areas. Thompson (1986) showed that voles had very low densities in 40-50 year old Sitka spruce in North Wales.

Restocked areas provided the major grassy habitat (ungrazed by domestic stock) in both study areas. For instance, within Kielder District Forest the clear-felling and restocking programme in the late 1980s had reached over 1000 ha/annum (Table 3.14) and was still increasing. Over a ten-year period this would create over 10,000 ha suitable for field voles. Such large, food rich areas have important implications for all microtine predators, including tawny owl. At the present time many large even-aged forests are being restructured at the end of the first rotation to provide a mosaic of different aged blocks. Assuming rotation lengths of 45-55 years, then around 20% of any forest could comprise good vole habitat at any one time.

The only published study of small mammal communities on restocked sites in spruce forests gives a mean field vole density of 31.1 per ha (Thompson 1986). This compares to 50-130 per ha in newly afforested areas in south Scotland (Charles 1981). Thompson also recorded a mean density of 15.7 per ha for bank voles and 6.2 per ha for wood mice on the same restocked sites. However, the vegetation of these areas may well have differed from the predominately grassy sites in the present study, where wood mice and bank voles formed a very small part of the small mammal

community in the trapping areas. Both of the latter species were more abundant in Glenbranter (Figure 3.8) and this was reflected in the diet of tawny owls (Table 3.3).

Although the field vole was the most abundant species caught in both trapping areas, it was interesting that the vole population dynamics were so different in the two study areas (Figure 3.12), where habitat appeared similar. However, the vole abundance data were from a relatively short period in time (1984-1990), and it is unclear just how representative these data would be of a longer timespan. The peak vole years in 1984, 1987 and 1990 at Kielder suggested a cycle length of three-years. But in Glenbranter, with annual fluctuations at a lower level and amplitude, it was unclear whether the apparent peaks in 1986 and 1990 represented one phase of a four-year cycle or just random annual fluctuations.

The dynamics of field vole populations throughout Europe show great variability. For instance, in Scandinavia there is a trend from non-cyclic populations in southern Sweden (Erlinge *et al.* 1984; Erlinge *et al.* 1988) to highly cyclic populations in northern Finland where both the amplitude and length of cycles increase with latitude with little evidence of cycles occurring south of latitude 56 N (Korpimäki 1986a; 1986b; Hansson and Henttonen 1985; Hanski *et al.* 1991). Kielder (55 N) and Glenbranter (56 N) therefore lie in the transition zone between cyclic and non-cyclic vole populations in Scandinavia.

Much debate still continues about the causal effect of vole cycles (Krebs 1985; Erlinge *et al.* 1988; Korpimäki and Norrdahl 1989; Lambin and Krebs 1991). Both extrinsic factors (such as predation and habitat quality) and intrinsic factors (such as changes in reproduction, mortality and dispersal) or a combination of both have been implicated. The role of predators in vole cycles has been increasingly studied.

Evidence now suggests that resident generalist predators (such as fox *Vulpes vulpes*, tawny owl and buzzard *Buteo buteo*) that can switch to alternative prey when voles are scarce, may prevent vole populations from becoming cyclic by increasing the level of predation on voles once they start to increase, to the point where vole numbers then decrease. This appears to be the case in southern Sweden (Erlinge *et al.* 1988). In northern Scandinavia generalist predators are scarce or absent, and voles can increase rapidly with little predation pressure (Hanski *et al.* 1991). Densities of specialist vole predators such as the weasel *Mustela nivalis* track vole cycles but with a time-lag, so their numbers are lowest when voles start to increase and highest when vole numbers are decreasing from the cycle peak. Such predation may accelerate the bottom end of the decline and deepen the trough in vole cycles but have little influence on vole numbers in the increase and peak phases. There is still much debate over what factor/s limit vole numbers at the peak of the cycle, resulting in a decrease. Korpimäki and Norrdahl (1991) have recently demonstrated that nomadic raptors such as kestrel *Falco tinnunculus*, short-eared owl and long-eared owl can respond both numerically and functionally to increasing vole numbers. This pooled predation on *Microtus* was shown to be positively density-dependent.

Few data are available on the overall impact of predators on field voles in Kielder and Glenbranter. However, it is interesting to note that Kielder (with a cyclic vole population) has fewer generalist predators than Glenbranter. Wild cat *Felix sylvestris*, and a high density of buzzards occur in Glenbranter but are absent from Kielder. Both species feed largely on voles when abundant and switch to alternative prey when voles are scarce. Other evidence from Scandinavia which is used to support the role of predators on vole cycles, is the synchronous fluctuations in vole and shrew populations (Korpimäki 1986a). In contrast, fluctuations in vole and shrew numbers were not synchronised in either of my trapping areas (Figures 3.7 and 3.8).

Small mammal trapping is a very time consuming way of assessing the dynamics of vole populations, so it was valuable that one of the vole sign indices (FCI) could be used to quickly assess the relative abundance of voles throughout both study areas. A number of previous studies have evaluated the relations between vole sign indices and vole abundance (Tapper 1976). Tapper (1979) used a vole sign index comprising both fresh grass clippings and fresh faeces. His index accounted for 83% of the variation in field vole density. Hansson (1979) also explored the relationships between trap catches and signs made by field voles in abandoned fields in Sweden. An index based on fresh grass clippings gave the best correlation with trap catches in both spring ($r=0.81$, $P<0.001$) and autumn ($r=0.87$, $P<0.001$). Indices using fresh droppings and runways gave a much weaker relationship. These results were very similar to mine. In contrast, Village and Myhill (1990) were not so successful, largely because field voles, wood mice and bank voles, were abundant in their study areas. They suggested that sign indices may be more useful when only one vole species was present (Tapper 1979; Hansson 1979; present study). The vole sign method used in my study did give a quickly-calculated measure of relative abundance of field voles throughout each study area, which was then used to explain intra- and inter-year variations in tawny owl performance (Chapters 5-8).

3.5 Summary

1. Analysis of nearly 1000 pellets containing over 2500 prey items showed that field voles were by numbers and biomass the most important item in the diet of adult tawny owls in both Kielder and Glenbranter.

2. In Kielder, field voles showed a seasonal decline in the diet of adult owls from a peak in December-March to a low point in May-July. This was compensated by an increase in common shrews and frogs.

3. In Kielder, a comparison from pellets of the diet of tawny owls with long-eared, short-eared and barn owls showed that field voles were the most important prey of all species. Long-eared and short-eared owls took more field voles than tawny owls and barn owls took less. Common shrews were the other major food item for all species, but tawny owls were unique in taking frogs and beetles.

4. Over 1200 prey were identified in tawny owl nests during the nesting period in both study areas. Field voles and birds were the most important items both in numbers and weight. Bird prey featured more from nests in Glenbranter.

5. The proportion of field voles in the prey brought to nests showed great annual fluctuations, ranging from 16.7% in 1989 to 85.3% in 1987 in Kielder. There was less annual variation in Glenbranter.

6. The proportion of field voles in the prey brought to nests was positively correlated ($r=0.903$, $n=12$, $P<0.001$) to spring vole abundance (with study areas combined).

7. The relative abundance and community structure of small mammal populations were quantified on one restocked site in each study

area by trapping. Trapping was done in March, May-June and September from May-June 1984 to May-June 1990 and comprised over 20,000 trap nights.

8. Field voles were the most abundant small mammal caught (over 75% of captures in both study areas), followed by common shrews. Wood mice and bank voles were caught infrequently but were more abundant in Glenbranter, resulting in significant difference in the small mammal community between trapping areas.

9. There were seasonal differences in the relative proportions of small mammals trapped. Field voles comprised most of the captures in March and fewest in May-June; numbers in September fell in between. The balance was made up largely by common shrews.

10. Within each trapping area, various vole sign indices were measured. An index using fresh grass clippings (FCI) in vole runs gave the best correlation with the trapping index (VTI). This relationship changed between the March and September trapping sessions due to faster decay rates of grass clippings in summer. Regression analysis was used to seasonally adjust the FCIs.

11. Seasonally adjusted FCIs from widely scattered restocked sites in both study areas were used to quantify spatial and temporal fluctuations in field vole abundance throughout each study area.

12. The amplitude of annual changes in the relative abundance of field vole was greater and at a higher level in Kielder, than in Glenbranter where seasonal increases from spring to autumn were more pronounced. A three-year cycle length of vole abundance was indicated at Kielder. In Glenbranter it was unclear whether vole populations were fluctuating on a regular multi-annual cycle.

CHAPTER 4

DISTRIBUTION AND OCCUPANCY OF TERRITORIES

4.1 Introduction

Both sexes of tawny owl *Strix aluco* spend the whole year within a relatively small territory that is strongly defended against neighbouring pairs (Chapter 1). The territory provides all of the owl's requirements, not only for breeding but also outside the breeding season. Considering the abundance of tawny owls in Britain, there is a dearth of information on their distribution and density. The most detailed information comes from a 13-year study in Wytham Wood, Oxfordshire (Southern 1970; Hirons 1985b). Hirons (1985b) provides the only study in coniferous woodland, from census work in November 1973 and 1974 in the Forest of Ae in south Scotland. More information is available from European studies (see reviews in Mikkola 1983; Cramp 1985; Galeotti 1990). However, virtually all long-term studies of 10 or more pairs were in broadleaved woodland, farmland or urban areas.

Newton (1979) stated that "in any landscape, an upper limit to the number of established raptor pairs is set by food or nest sites, which ever is in shortest supply". In this chapter I describe the distribution of tawny owls in spruce *Picea* spp. forests in Kielder and Glenbranter (Chapter 2), explore whether nest sites limited density, and what factors were responsible for the observed population increases in both study areas.

4.2 Methods

4.2.1 Nestboxes

Nestboxes (Plate 4.1) suitable for tawny owls were erected in both the Kielder and Glenbranter areas from the start of the study. Nestboxes were used instead of attempting to work with owls using natural nest sites because:

A. Natural nests were difficult to locate in coniferous forests.

B. It was impossible to catch most breeding adults in natural sites.

Plate 4.1 Tawny owl nestbox, showing the siting of a box (upper) and close-up (lower).

C. The quality of natural nest sites varied greatly. Nest site quality may have influenced reproductive success and this aspect would have been difficult to control. Nestboxes provided a nest site of almost equal quality for each pair.
D. There was little evidence to suggest that nestboxes affected the density of territorial pairs (Southern 1970).

The nestboxes were a standard design developed for this study (Figure 4.1). The boxes were made from 25 mm thick, rough-sawn softwood timber, except for the tops which were made from 9 mm thick exterior grade plywood. The front and back were made from two planks joined with 20 mm X 6C corrugated fastners and all the joints were nailed. The fixing board was attached to the box with 100 mm nails, the ends of which were turned over to prevent them being pulled out once the box was erected. Drainage gaps of 5 mm were left between the boards in the bottom of the box. The exterior was treated with two coats of brown Cuprinol preservative, while the interior was left untreated. These boxes differed substantially from the long chimney-type box slung beneath leaning boughs of broadleaved trees (Flegg and Glue 1971) and used in the study of Southern (1970).

Inside each box a 100-150 mm layer of dry conifer needle litter was provided to allow the bird to form a scrape for its eggs. This layer became fouled after young were produced, and was replaced once the chicks had fledged. Access to the box for checking the contents and replacing the litter was via the entrance hole.

Nestboxes were placed on trees at heights of 1.6-5.2 m (but mainly at 3.0-3.5 m) measured from the ground to the base of the box. They were fixed to the trunk in a vertical or slightly forward leaning position with copper or light alloy roofing nails. Nestboxes were sited to allow the owls a clear flight path to the box, either through thinned stands or other openings such as racks, rides, watercourses, felled areas and windblown trees.

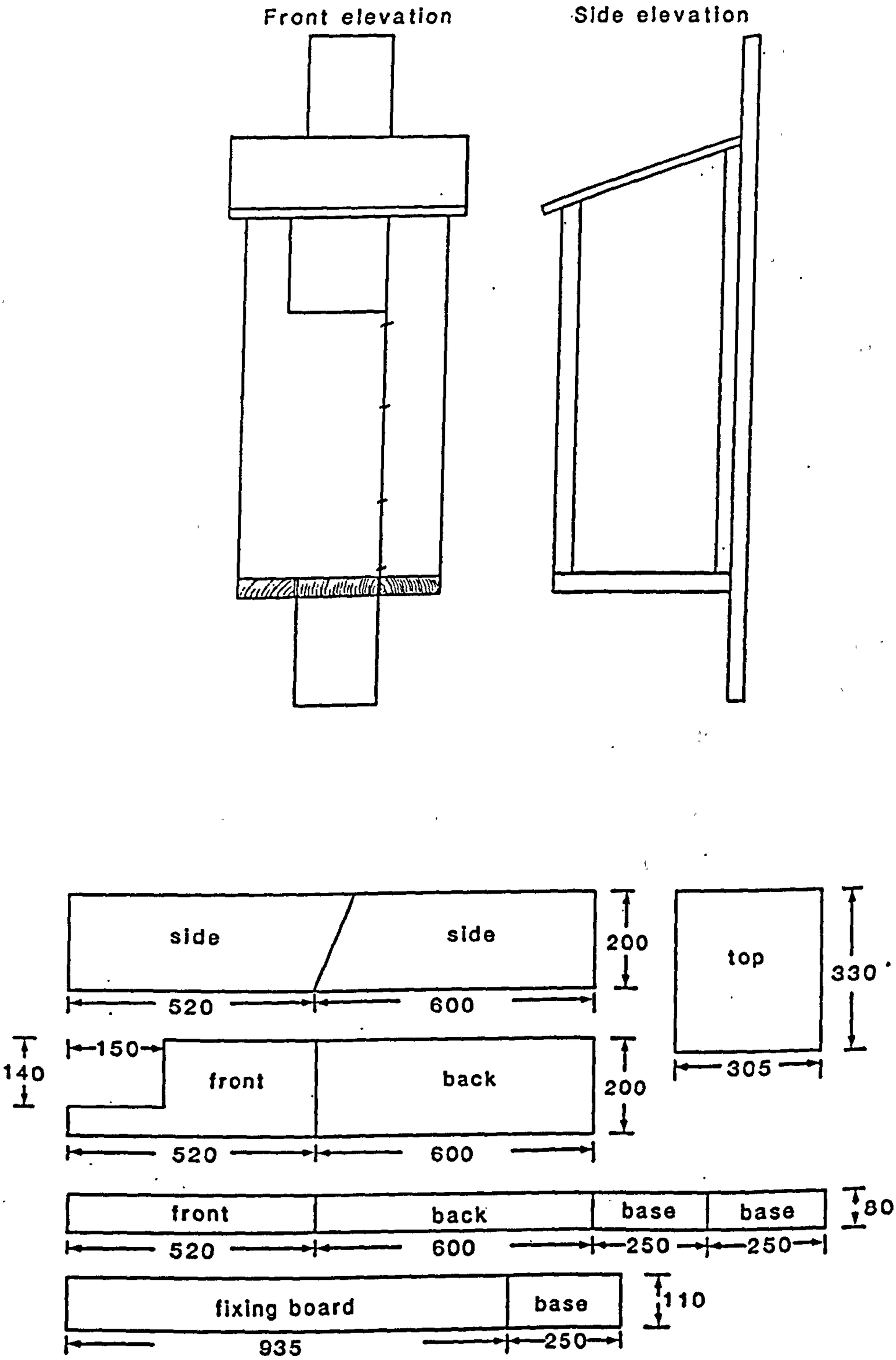


Figure 4.1 Front and side view of the tawny owl nestbox used in the study (upper) together with a cutting list giving the dimensions (lower). Details of the boxes construction are given in the text (also see Petty 1987b).

In Kielder, nestboxes were originally spaced so that one box was available near the centre of each owl's territory identified prior to the start of the project, with one additional box between territories. Having twice as many nestboxes as pairs ensured that any increase in the breeding population was quickly detected. This placement of boxes resulted in approximately 400 m between boxes along valley sytems where the original owl territories were located. Additional boxes were erected in other areas that appeared suitable for owls but which lacked pairs. In Glenbranter, no information was available on the spacing of owl territories at the start of the study, so boxes were erected at a similar spacing (400 m) to those in Kielder.

The number of nestboxes available each year varied because boxes were removed (and often re-sited) as areas were felled. Occasional extensions were also made to each study area to take in additional pairs of owls. The number of boxes available in Kielder increased to a peak of 167 in 1986 and then declined slightly to 153 by 1991 (Table 4.1). In Glenbranter the number increased to 142 in 1990 and then declined slightly. The average number of boxes available per occupied owl territory ranged from 1.8 (1980) to 3.4 (1986) in Kielder, and 2.5 (1991) to 3.8 (1984) in Glenbranter. Overall there were slightly more boxes available for each occupied territory in Glenbranter (3.1) than in Kielder (2.6). The important point is that there were far more boxes available each year than there were pairs of tawny owls.

Other birds used the nestboxes for breeding; namely redstart *Phoenicurus phoenicurus*, great tit *Parus major*, starling *Sturnus vulgaris* and goosander *Mergus merganser* in both study areas; coal tit *Parus ater* and stock dove *Columba oenas* in Kielder and mandarin duck *Aix galericulata* in Glenbranter. All except goosander bred much later than tawny owls and did not compete with the owls for nest sites. Most goosanders commenced laying after tawny owls, but there was some overlap in clutch initiation and a few instances

Table 4.1 The number of nestboxes available and number of occupied territories of tawny owls in each study area.

Year	Kielder			Glenbranter		
	Boxes available	Pairs of owls *	Boxes per pair	Boxes available	Pairs of owls *	Boxes per pairs
1980	48	26	1.8	-	-	-
1981	90	44	2.0	-	-	-
1982	96	42	2.3	-	-	-
1983	112	39	2.9	88	?	?
1984	118	46	2.6	87	23	3.8
1985	131	50	2.6	90	25	3.6
1986	167	49	3.4	106	28	3.8
1987	162	56	2.9	110	35	3.1
1988	160	61	2.6	141	40	3.5
1989	161	52	3.1	136	51	2.7
1990	158	64	2.5	142	52	2.7
1991	153	66	2.3	138	56	2.5
Kielder 81-91	1556	595	2.6			
Glenbranter 84-91				951	310	3.1

Available boxes were those in place up to 31 March each year.

** From Table 4.5 column C*

of tawny owls and goosanders laying at the same time in the same boxes. However, in all the owl territories where goosanders also bred there were always more than two nestboxes, so the resident owls should never have lacked a box.

The only mammal to use nestboxes was the red squirrel *Sciurus vulgaris*. Up to 30% of the avialable nestboxes each year in Glenbranter and 15% in Kielder contained stick dreys. Some of these were substantial and reduced the entrance hole so much that it is doubtful whether tawny owls could have entered. Less substantial stick dreys were flattened by tawny owls or goosanders prior to laying. To overcome the problem of some nestboxes not being available for tawny owls, all stick dreys were removed under licence from the boxes prior to the breeding season unless they contained young squirrels (up to 3 boxes per spring in Glenbranter only).

4.2.2 Measurements of owl territories

The distribution of tawny owl territories in Kielder was determined prior to the erection of nestboxes. This was done during 1975-78 when the area was repeatedly searched for breeding sparrowhawks (Petty 1979) and signs of occupied owl territories were also recorded from roost/pellet stations, nest sites, fledged broods or moulted feathers. Forty territories were located.

After the erection of nestboxes, most of the breeding females were caught each time they bred (Chapter 6). After the first year many of the captured owls were of known identity, having been ringed in the past as breeding females or chicks. Over the years it was possible to determine groups of nestboxes and natural nest sites that were used by individual females. For present purposes each group was considered to form one "nesting territory". During the study 71 nesting territories were used in Kielder (1979-91) in the same area where 40 nesting territories had previously been located, and 58 in Glenbranter (1983-91).

The centre of each nesting territory was fixed at the nest site when only one was used, or at the mid-point between nests when more than one had been used. The nearest neighbour distance (NND), used to measure the spatial distribution of owl territories in 1991, was the linear measurement from the centre of one nesting territory to the centre of its nearest neighbour (Newton *et al.* 1977). NND were only calculated for those nesting territories where there was suitable nesting habitat (including nestboxes) between neighbours. The size of each nesting territory was calculated from the area of a circle with a radius of half the NND. The altitude of each nesting territory was also measured at the centre from 1:50,000 scale OS maps.

4.2.3 Occupancy of territories

Prior to egg laying, each pair of owls visited several potential nest sites in their territory. Signs from these visits included

traces of down or small body feathers adhering to the entrance hole. These signs occurred up to one month before the first egg was laid. Closer to laying a deep scrape was formed in the debris at the bottom of the chosen nest site, often with down and small body feathers around the edge. In years when pairs did not produce eggs (Chapter 5), they still went through this process, creating a well formed nest scrape.

A nesting territory was classified as occupied when a fresh scrape, with down and/or small body feathers, was found in at least one nest site. Territories were regarded as unoccupied when no signs of owls were found at any of the nest sites during the last two weeks of March and the first two weeks of April. Tawny owls did not roost in the nestboxes in either study area during the winter, so all signs of owls in the boxes were related to breeding behaviour. Further evidence that these territories were unoccupied came in subsequent years when they were re-occupied and the adults caught. The original adults had always disappeared (presumed dead) and had been replaced by birds breeding for the first time, but in a few instances vacancies were filled by adults moving from nearby territories (Chapter 6).

4.3 Results

4.3.1 Nest sites

Information on the type of "natural" nest sites (excluding nestboxes) used by tawny owls came from 57 nests located in or near to the Kielder study area during 1975-90 (Table 4.2). Tree cavities of various types comprised 38.6% of these sites (Plates 4.2-4.4), crag (Plate 4.5) and ground nests (Plate 4.6) comprised 26.3%, man-made structures (Plate 4.7) 22.8% and disused stick nests of other species 12.3%. These data were probably biased towards the most easily found nest sites. Crow *Corvus corone* nests and ground sites used by tawny owls were particularly difficult to locate.

Table 4.2 Natural nest sites used by tawny owls in or near to the Kielder study area from 1975-1990.

Nest site	Frequency (%)
Tree hole, covered	13 (22.8)
Tree hole, open	6 (10.5)
Tree crotch, open	3 (5.3)
Crow nest	5 (8.8)
Goshawk nest	2 (3.5)
Crag ledge	5 (8.8)
Ground	10 (17.5)
Building (inside)	8 (14.0)
Hay stack	4 (7.0)
Deer high seat	1 (1.8)
Total	57(100.0)

** All sites were at the base of a tree (Plate 4.6)*

Table 4.3 Nest sites in which tawny owls laid eggs in Kielder (1979-83), showing the response of owls to the provision of nestboxes. Nestboxes were first avialable for the 1980 breeding season. All pairs had switched to breeding in nestboxes by 1983 and continued thereafter apart from one nest in a tree hole.

Nest site	Year					
	1979	1980	1981	1982	1983	1984
Nestbox	0 (0.0)	15 (83.3)	36 (87.8)	31 (91.2)	10(100.0)	43(100.0)
Tree hole, covered	1 (12.5)	2 (11.1)	1 (2.4)	1 (2.9)	0 (0.0)	0 (0.0)
Tree hole, open	2 (25.0)	0 (0.0)	1 (2.4)	1 (2.9)	0 (0.0)	0 (0.0)
Tree crotch, open	1 (12.5)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Crow nest	0 (0.0)	0 (0.0)	1 (2.4)	0 (0.0)	0 (0.0)	0 (0.0)
Crag ledge	1 (12.5)	0 (0.0)	1 (2.4)	0 (0.0)	0 (0.0)	0 (0.0)
Ground	2 (25.0)	1 (5.6)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Deer high seat	1 (12.5)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Barn	0 (0.0)	0 (0.0)	1 (2.4)	1 (2.9)	0 (0.0)	0 (0.0)
Total	8(100.0)	18(100.0)	41 (99.8)	34 (99.9)	10(100.0)	43(100.0)

Plate 4.2 Tawny owl nest site; a closed tree hole in an alder Alnus glutinosa.

Plate 4.3 Tawny owl nest site; an open tree hole in a Norway spruce Picea abies.

Plate 4.4 Tawny owl nest site; a tree crotch in a sycamore Acer pseudoplantanus.

Plate 4.5 Tawny owl nest site; a crag ledge, the nest is near the persons hand.

Plate 4.6 Tawny owl nest site; a typical ground nest against the butress of a Norway spruce. These nests are very difficult to locate when the female is sitting due to her cryptic colouration.

Plate 4.7 Tawny owl nest site; in the roof cavity of a disused farm house.

Nestboxes were first erected in Kielder during the winter of 1979/80. In the first year (1980) with boxes available, 83% of the nesting attempts were in boxes and by 1983 all the natural sites in the study area had been abandoned (Table 4.3). Subsequently (1984-91) only one natural nest site (covered tree hole) was used in 317 layings.

Unfortunately only a few females were caught at natural nest sites to investigate individual responses to nestboxes. Two females were caught at ground nests in 1979 and ringed. Nestboxes were erected in both territories in November/December 1979. One female switched to breeding in a box in 1980 and for each breeding attempt up to 1991, while the other changed to a box in 1981 and for each breeding attempt up to 1985 after which she died. Another female was caught at a crag ledge site in 1981, possibly the same female that had bred there in 1980, even though a box was available from January 1980. The female bred in the box for the first time in 1982 and subsequently up to 1985 after which she died. The replacement females (1986-1991) never used the crag sites, even though at least three ledges on two seperate crags had been used in the past. At a site with two tree holes (one covered and one open) and a box erected in November 1979, the female bred in a tree hole in 1979 and 1980. In 1981 she used one tree hole followed by the box and then the other tree hole in three nesting attempts, the first two having failed during egg-laying. In 1982 she first used the box and deserted the eggs, and subsequently reared chicks from a tree hole. This female died and was replaced after 1982. The covered tree hole collapsed and no subsequent breeding attempts up to 1991 occurred in the open tree hole, only in nestboxes. These observations suggest that the switch to breeding in nestboxes was achieved by the existing females changing nest sites rather than by a new generation of females starting their first breeding attempts in nestboxes.

Few similar data were available on the use of natural nest sites in Glenbranter. The natural sites that were located in and near to the study area were either in tree holes, crow nests, on the ground or in buildings. However, in parts of the study area, crags with suitable ledges and cavities for breeding were abundant and it was suspected that tawny owls used such sites prior to nestboxes being available. Nestboxes were erected for the first time during the 1982/83 winter after which only one nesting attempt was subsequently located in a natural site (open tree hole).

By 1981 in Kielder and 1984 in Glenbranter most of the pairs being monitored were breeding in nestboxes. It was unlikely that pairs regularly bred undetected in natural sites in either study area after this. Occasionally short-lived territories may have been established using natural sites, but I considered this unlikely. Once breeding became regular in nestboxes I had no indication that pairs ever reverted to natural sites.

4.3.2 Number of owl territories monitored

By 1981 in Kielder and 1984 in Glenbranter most of the existing territorial population of tawny owls had switched to breeding in nestboxes. Since then the number of territories monitored has increased in both areas (Table 4.4). These additional territories can be placed into two categories. First, both study areas were enlarged slightly to include additional pairs. This represented nine additional territories in Kielder during the period 1982-1987, and 16 territories in Glenbranter during 1987-1989. Second, the population has slowly increased within both study areas due to the establishment of new territories, 17 in Kielder (1982-91) and 19 in Glenbranter (1985-91). All these new territories were established either in areas where nestboxes had been available but unoccupied in the past or where a new pair settled between existing pairs and took over a box used by a neighbouring pair in the past. As a result the number of territories monitored in Kielder increased

Table 4.4 Number of tawny owl territories monitored annually in Kielder and Glenbranter.

Year	Territories monitored	Existing territories		New territories (%)
		Monitored in previous year (%)	Monitored for first time (%)	
(A)	(B)	(C)	(D)	(E)
Kielder				
79	8	8 -	-	-
80	29	29 -	-	-
81	45	45 -	-	-
82	48	45 (93.8)	1 (2.1)	2 (4.2)
83	50	48 (96.0)	1 (2.1)	1 (2.0)
84	54	50 (92.6)	3 (5.6)	1 (1.9)
85	56	54 (96.4)	2 (3.6)	0
86	58	56 (96.6)	1 (1.7)	1 (1.7)
87	62	58 (93.5)	1 (1.6)	3 (4.8)
88	66	62 (93.9)	0	4 (6.1)
89	66	66(100.0)	0	0
90	68	66 (97.1)	0	2 (2.9)
91	71	68 (95.8)	0	3 (4.2)
79-91	681	655	9	17
Glenbranter				
83	5	5 -	-	-
84	23	23 -	-	-
85	27	23 (85.2)	0	4(14.8)
86	30	27 (90.0)	0	3(10.0)
87	37	30 (81.1)	5(13.5)	2 (5.4)
88	44	37 (84.1)	4 (9.1)	3 (6.8)
89	54	44 (81.4)	7(13.0)	3 (5.6)
90	57	54 (94.7)	0	3 (5.3)
91	58	57 (98.3)	0	1 (1.7)
83-91	335	300	16	19

The initial development of the study in Kielder (1979-81) and Glenbranter (1983-84) saw a rapid increase in the monitoring of existing pairs (C). Thereafter the monitored population increased slowly by either established pairs being monitored for the first time as the study area increased (D) or by new territories being established within the existing study area (E).

from 45 in 1981 to 71 in 1991, and in Glenbranter from 23 in 1985 to 58 in 1991.

4.3.3 Occupancy of territories

The overall occupancy of the owl territories monitored was significantly higher (chi-squared with Yates correction = 6.83, df=1, P<0.01) in Glenbranter (94%) than Kielder (88%) (Table 4.5). There was also more variation in annual occupancy rates in Kielder, ranging from 78% (1983) to 94% (1990), but in Glenbranter from only 90.9% (1985) to 96.6% (1991) (Table 4.5).

In Kielder the number of occupied territories increased from 44 in 1981 to 66 in 1991. The annual rate of increase varied greatly, with declines occurring in some years (Table 4.5). In Glenbranter the number of occupied territories increased from 23 in 1984 to 56 in 1991. Here the rate of increase was much steadier than in Kielder. Overall the number of occupied territories increased by 4.5% per annum in Kielder and 13.9% in Glenbranter (Table 4.5). This was after increases due to expansion of the study area had been allowed for (Table 4.5).

Annual variation in occupancy was significantly related to field vole *Microtus agrestis* abundance in Kielder (Table 4.6). In low vole years occupancy averaged 81%, compared to 90-91% in increasing and decreasing vole years. Occupancy rates in increasing and decreasing vole years were therefore similar to those in Glenbranter. There was less variation in vole abundance in Glenbranter where it was not possible to assign years to vole abundance classes as in Kielder (Chapter 3).

The records for individual territories showed that far more territories were unoccupied in consecutive years in Kielder than in Glenbranter. In Kielder during 1984-91, four territories were unoccupied for four or more years and three territories for three years. In Glenbranter during the same period, the greatest number

Table 4.5 Annual occupancy and changes in the number of occupied tawny owl territories in Kielder (1981-91) and Glenbranter (1984-91).

Year	Number of territories monitored	Occupancy of territories		Population change since previous year			
		Occupied (%)	Unoccupied (%)	Net occupied territores	Net occupied territories in previous year	Change in occupied territories	
(A)	(B)	(C)	(D)	(E)	(F)	n(E-F)	%(n/F*100)
Kielder							
81	45	44 (97.8)	1 (2.2)	44	-	-	-
82	48	42 (87.5)	6(12.5)	41	44	-3	(-6.8)
83	50	39 (78.0)	11(22.0)	38	41	-3	(-7.3)
84	54	46 (85.2)	8(14.8)	43	38	5	(13.2)
85	56	50 (89.3)	6(10.7)	48	43	5	(11.6)
86	58	49 (84.5)	9(15.5)	48	48	0	(0.0)
87	62	56 (90.3)	6 (9.7)	55	48	7	(14.6)
88	66	61 (92.4)	5 (7.6)	61	55	6	(10.9)
89	66	52 (78.8)	14(21.2)	52	61	-9	(-14.8)
90	68	64 (94.1)	4 (5.9)	64	52	12	(23.1)
91	71	66 (93.0)	5 (7.0)	66	64	2	(3.1)
82-91	599	525 (87.6)	74(12.4)	516	494	22	(4.5)
Glenbranter							
84	23	23(100.0)	0 (0.0)	23	-	-	-
85	27	25 (92.6)	2 (7.4)	25	23	2	(8.9)
86	30	28 (93.3)	2 (6.7)	28	25	3	(12.0)
87	37	35 (94.6)	5 (5.4)	30	28	2	(7.1)
88	44	40 (90.9)	4 (9.1)	36	30	6	(20.0)
89	54	51 (94.4)	3 (5.6)	44	36	8	(22.2)
90	57	52 (91.2)	5 (8.8)	52	44	8	(18.1)
91	58	56 (96.6)	2 (3.4)	56	52	4	(7.7)
85-91	307	287 (93.5)	20 (6.5)	271	238	33	(13.9)

Net occupied territories = Table 4.5 column (C) - Table 4.4 column (D).

Table 4.6 Occupancy of tawny owl territories in Kielder (1982-1991) in relation to vole year class.

Years	Vole year class	Territories		
		Occupied (%)	Unoccupied (%)	Total
83,86,89	Low	140(80.5)	34(19.5)	174
84,87,90	Increasing	166(90.2)	19 (9.8)	184
82;85,88,91	Decreasing	219(90.9)	22 (9.1)	241
All years		525(87.6)	74(12.4)	599

A significantly higher proportion of territories were occupied in increasing+decreasing than in low vole year classes (chi-squared with Yates correlation = 10.22, df=1, P<0.01).

Vole year classes are taken from Chapter 5 (Table 5.2).

Table 4.7 Comparison of altitude, nearest neighbour distance (NND) and estimated area of tawny owl territories in Kielder and Glenbranter in 1991.

Parameter	Kielder	Glenbranter
NND (km)		
n	69	58
mean	0.74	0.90
SE	0.03	0.04
median	0.74	0.84
range	0.38-1.60	0.54-2.04
Altitude (m ASL)		
n	71	58
mean	231.1	78.4
SE	4.41	6.30
median	220	70
range	190-350	20-210
Area (ha)		
n	69	58
mean	48.2	69.8
SE	4.33	6.47
median	43.0	55.4
range	11.3-201.1	22.9-326.9

There were significant differences in median altitude (Mann-Whitney U-test, Z=-9.56, P<0.001) and NND (Z=3.68, P<0.001) between study areas.

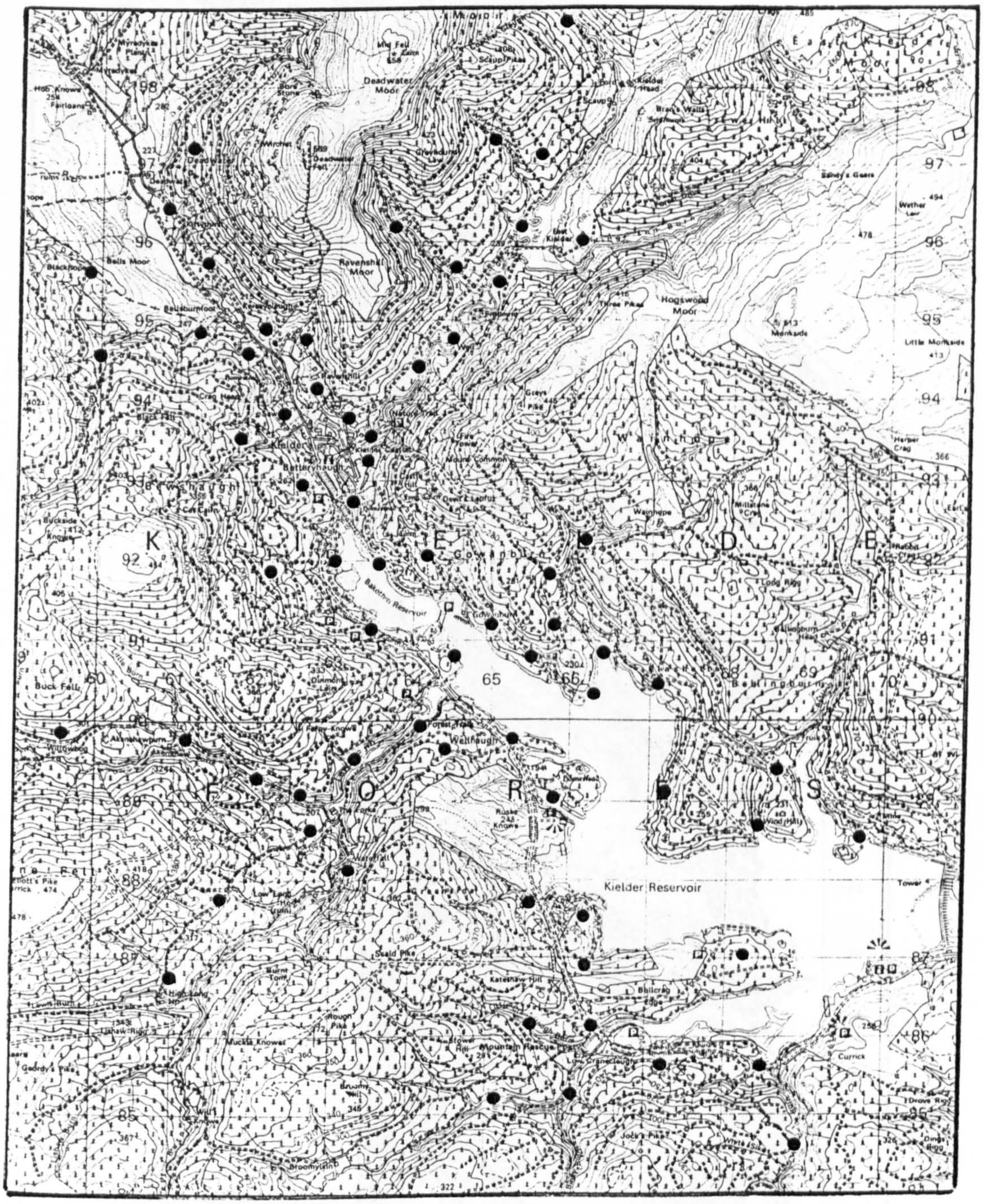
of years a territory was unoccupied was two. Three of the four territories with the lowest occupancy in Kielder were the highest territories at the heads of valley systems. Altitude at the centre of these territories was 300, 320 and 350 m, well above the median of 231 m for the study area.

4.3.4 Distribution of territories

In both study areas, nesting territories were regularly spaced along the lower ground in each valley system (Figure 4.2 and 4.3). Territories were at a significantly lower altitude in Glenbranter than Kielder (Table 4.7). This resulted from topographical differences between the areas and not from tawny owls selecting different altitudes in each study areas. Most of the territories in Glenbranter were below 100 m altitude whereas most in Kielder were over 200 m altitude (Figure 4.4). The flooding of the lower part of the Kielder study area for Kielder Water Reservoir truncated the range of altitudes in Kielder. Prior to the flooding the lowest altitude in the study area was 140 m, still much higher than most of the nesting territories in Glenbranter.

Nesting territories in continuous habitat were significantly closer together in Kielder, with a median NND of 0.74 km compared to 0.90 km in Glenbranter (Table 4.7 and Figure 4.5). This resulted in the median territory being smaller in Kielder (43 ha) than Glenbranter (55 ha).

There was no significant relationship between altitude of nesting territories and NND ($r=-0.11$, $df=126$, NS) with study areas combined. However a multiple regression model with NND as the dependent variable and altitude and study area as independent variables was significant and explained 18.0% of the variation in NND (Table 4.8). Adding a study area*altitude interaction to this model decreased the fit, demonstrating that the slopes of the individual study area models of NND on altitude were similar but the intercepts were different (Figure 4.6). This analysis suggested


Kielder Reservoir
Deadwater Moor
Ravenshill Moor
Hogswood Moor
East Kielder Moor
Bells Moor
Blackhope
Fairloans
Deadwater
Kielder
Butteryhaugh
Browshaugh
Bakethin Reservoir
Gowanburn
Falstone
Wellhaugh
Kielder Reservoir
Currick
Wood Hill
Three Pikes
Greys Pike
Mound Common
Deadwater Fell
Grey Burnhope Law
Sandy's Gears
Wether Law
Little Monkside
Harper Crag
Millstone Crag
Rabbit Crag
Lodge Rigg
Ballingburn Head
Bellingburn
Deadwater Fell
Kielder Castle
Nature Trail
Fire Tower
Castle Hill
Dewar's Leptut
Wainhope
Bakethin Reservoir
Gowanburn
Forest Falls
Akenshawburn
Willowbog
Ruske Knowe
Low Lewis Hope
Scald Pike
Burnt Tom
Katesnaw Hill
Rough Pike
Muckle Knowes
Tower Hill
Mountain Rescue Post
Low Cranecleughs
Broomylaw
Jock's Pike
Buck Fell
Little Burn
Diamond Law
Dimmon Hill
Deadwater Fell
Mirehet
Kielder Castle
Nature Trail
Fire Tower
Castle Hill
Dewar's Leptut
Mound Common
Wainhope
Millstone Crag
Rabbit Crag
Lodge Rigg
Ballingburn Head
Bellingburn
Three Pikes
Greys Pike
Harper Crag
Little Monkside
Monkside
Sandy's Gears
Wether Law
Bloodybush Edge
Bloodybush Head
Kielder Head
Scaup
Scaup Pikes
Brant's Walls

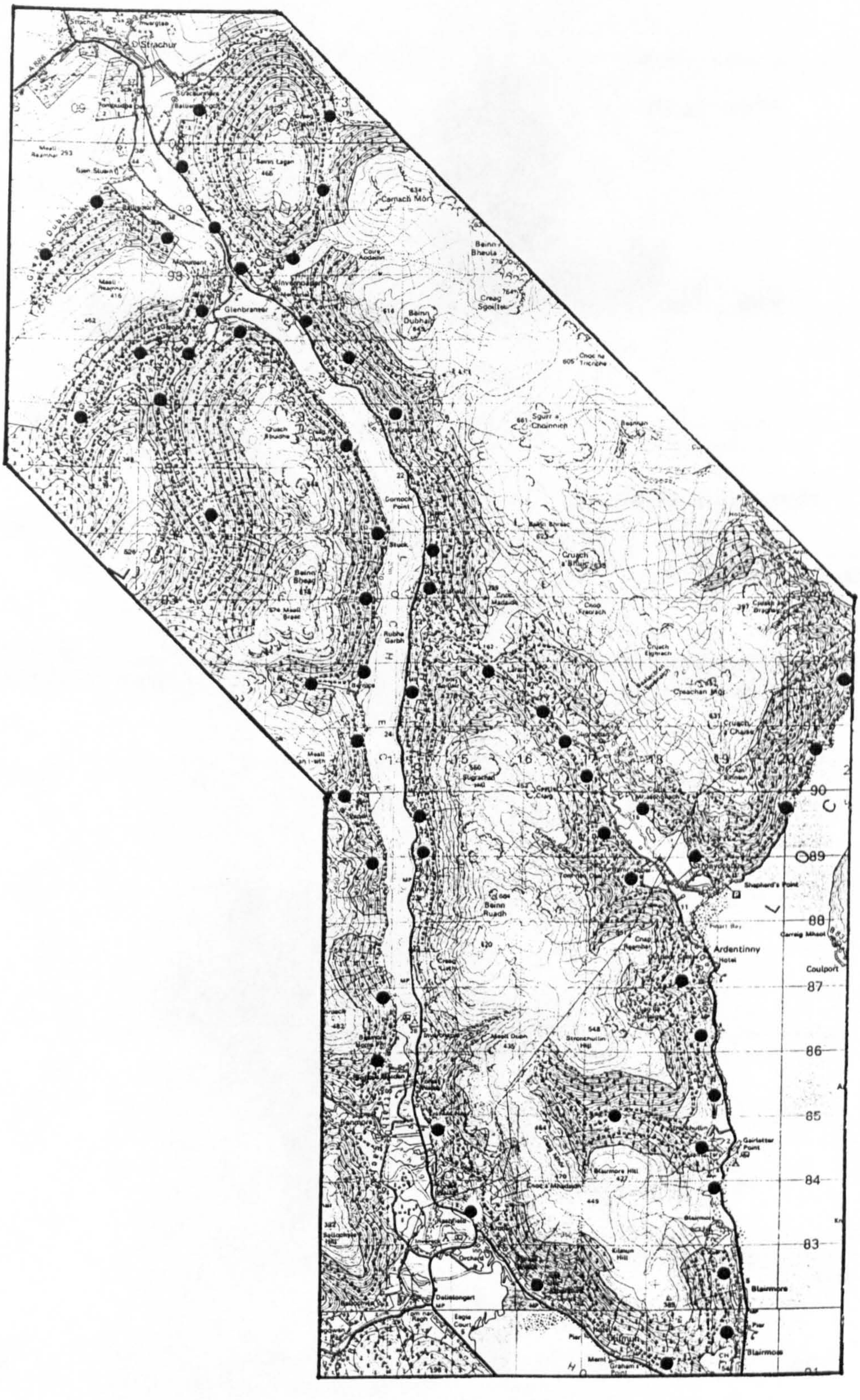


Figure 4.3 Distribution of tawny owl nesting territories in Glenbranter (● = centre of nesting territory).

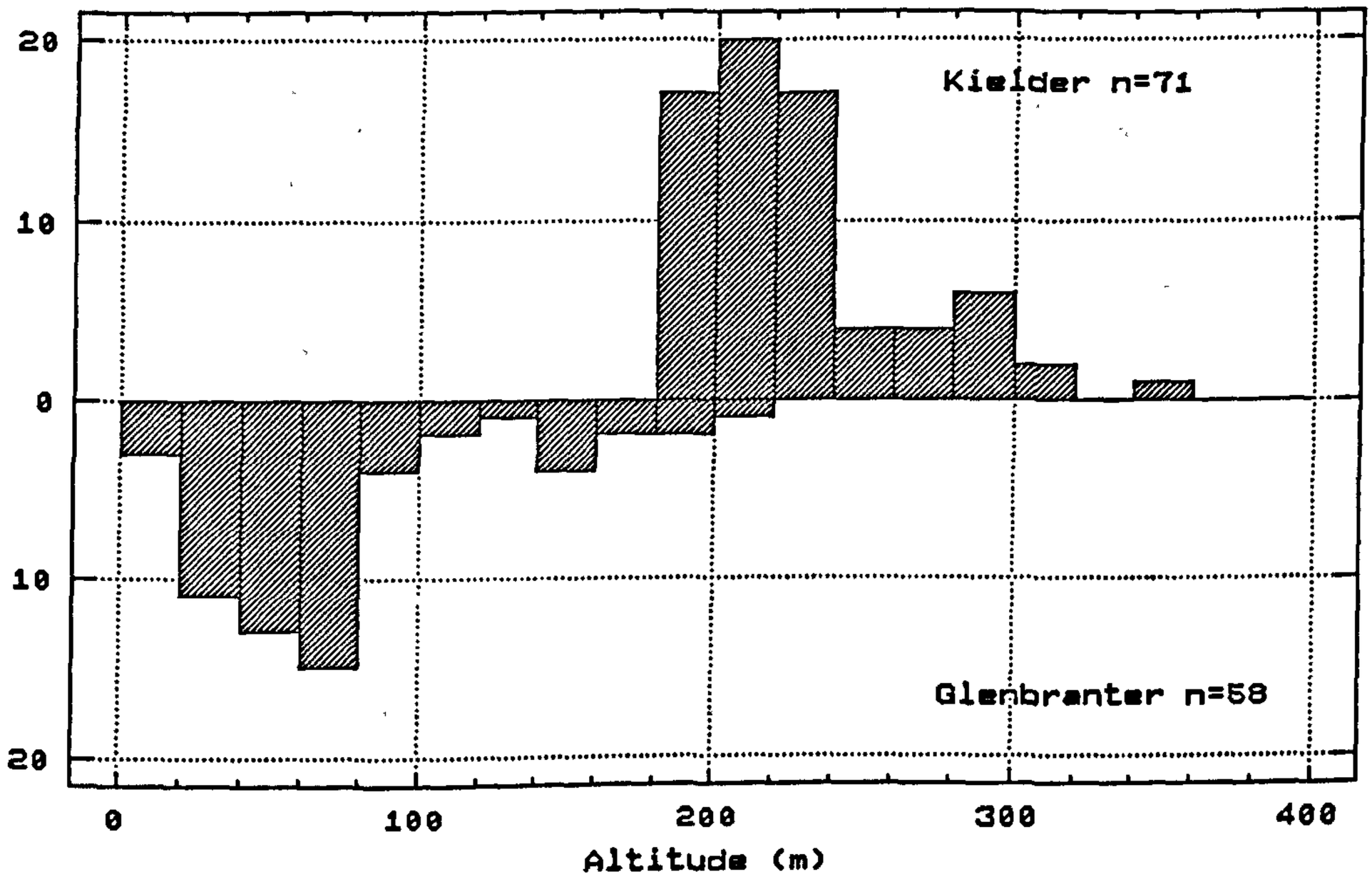


Figure 4.4 Altitude at the centre of tawny owl nesting territories in Kielder (upper) and Glenbranter (lower) in 25 m classes.

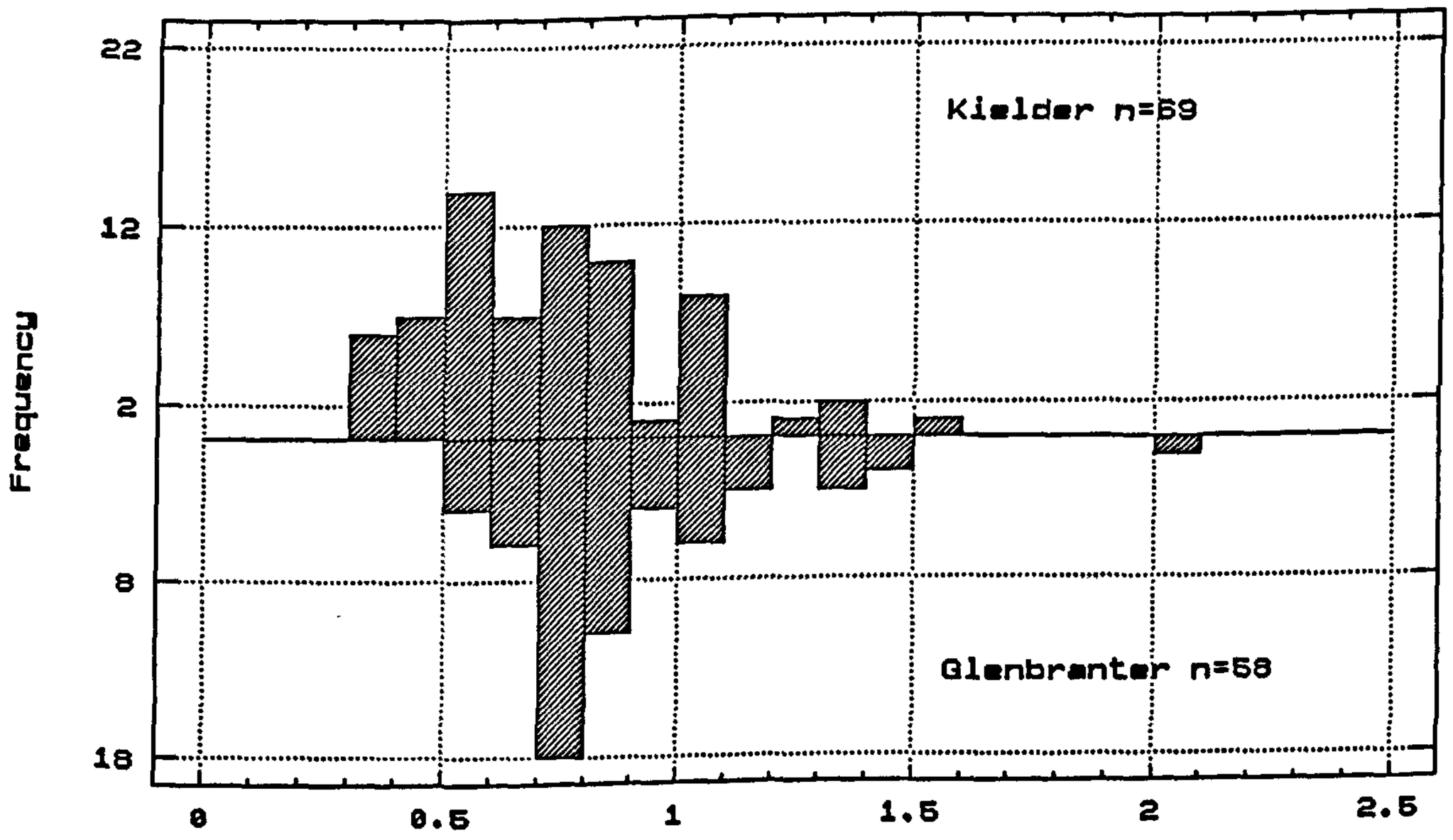


Figure 4.5 NND between nesting territories in Kielder (upper) and Glenbranter (lower) in 100 m classes.

Table 4.8 A multiple regression model using altitude and study area (as a factor) explained 18.0% of the variation in NND (F=13.59, df=2,124, P<0.001).

Independent variable	Coefficient	SE	t	Significance level
Constant	0.283	0.127	2.23	0.028
Altitude	0.002	0.001	3.70	0.000
Study area	0.467	0.093	5.02	0.000

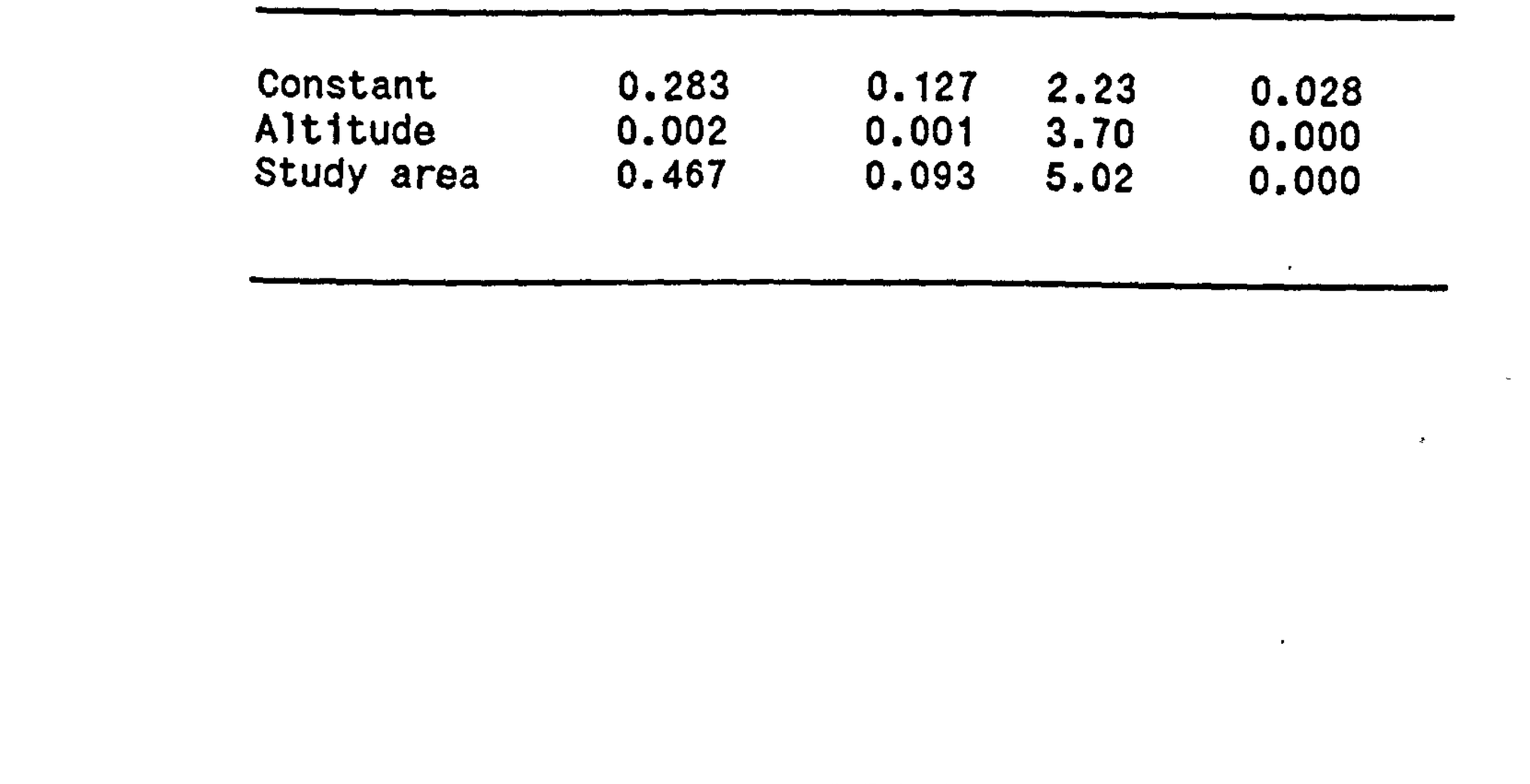


Figure 4.6 Scatter plots showing relationship between NND and altitude for each tawny owl nesting territory in Kielder (1) and Glenbranter (2). The lines are linear regressions for each study area (Kielder Y=0.201+0.002X, r-squared = 10.9%, df=68, P<0.01; Glenbranter Y=0.769+0.002X, r-squared = 9.4%, df=57, P<0.05).

that altitude did influence the density of tawny owls but only weakly and that some other factor/s were involved.

In a previous account, owl density was shown to be related to the spatial diversity of habitat (Petty 1989). Density was lower in tree stands of a single age and increased where clear-felling created a patchwork of good feeding areas (establishment and pre-thicket crops), with pole-stage crops suitable for roosting and breeding, and many edges from which to hunt. This can be demonstrated by comparing two areas of the same size (375 ha) in Kielder (Figures 4.7 and 4.8). Prior to 1983, both comprised mostly pole and thicket stage forest, one area had three pairs of tawny owls and the other had two pairs. By 1990/91 much clear-felling had broken-up the first area and the number of tawny owls had increased to 6 pairs (Figure 4.7). In the second area little change occurred and the numbers of owls had increased to three pairs, the additional pair having established near to the only clear-fell in this area (Figure 4.8).

4.4 Discussion

4.4.1 The use of nestboxes

Nestboxes have been used widely by ornithologists in population studies of cavity-nesting birds, particularly the blue tit *Parus caeruleus*, great tit *Parus major* and pied flycatcher *Ficedula hypoleuca* (see reviews in Lack 1954; Lack 1966; Perrins 1979; Lundberg and Alatalo 1992). Previous long-term studies of the tawny owl have also used nestboxes (Southern 1970; Delmée *et al.*1978; Wallin 1988). The main advantages of using nestboxes are that nest site quality can be standardized, seaching time is reduced, breeding data can more easily be collected and adults are often more easily caught. The main disadvantages are that it is often difficult to assess the impact that nestboxes have on breeding density, and breeding success may differ between natural and artificial sites. Together these aspects may alter the population dynamics of the species.

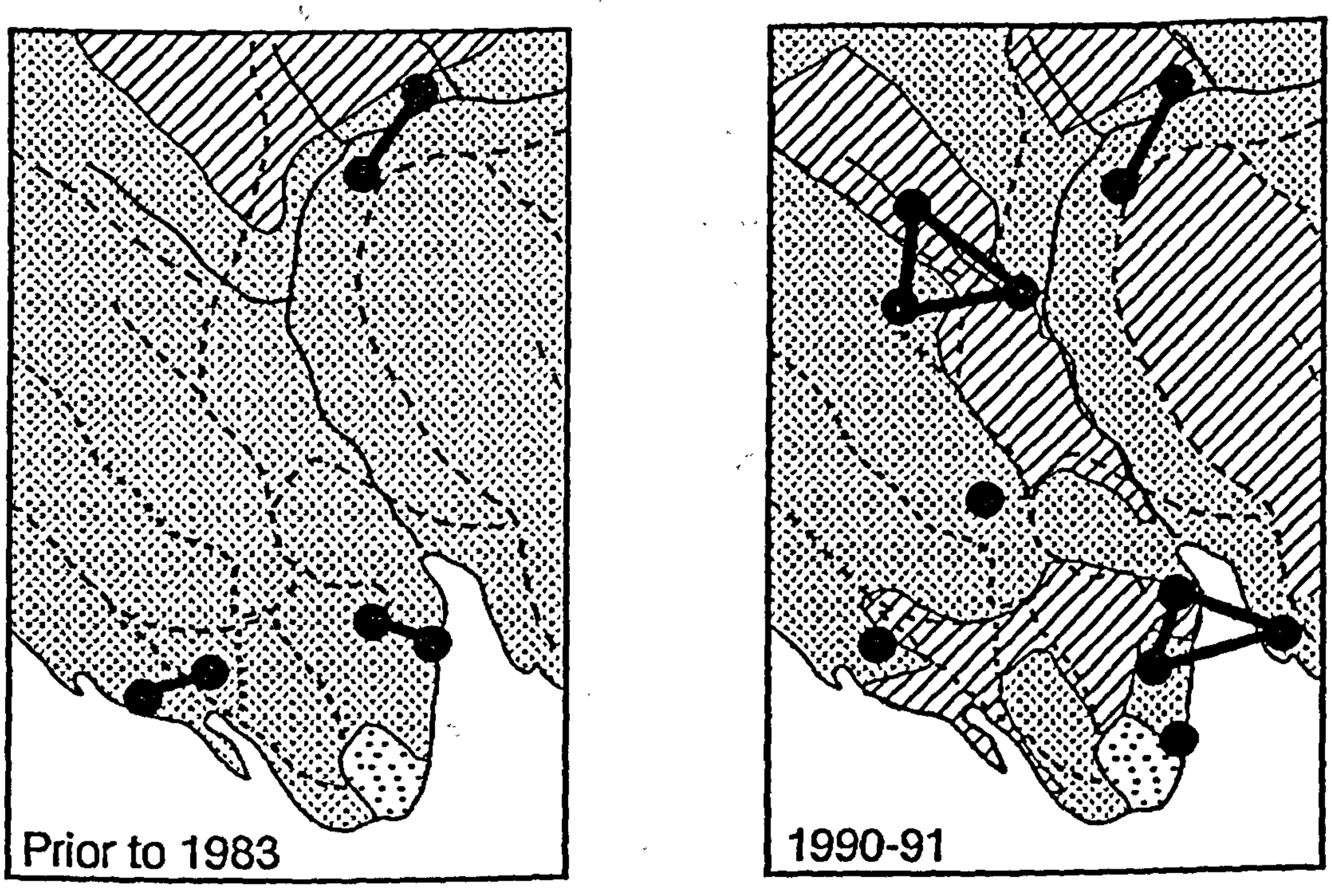


Figure 4.7 The Plashetts Burn area in the Kielder study area prior to 1983 (left-hand) and in 1990-91 (right-hand). The black circles joined by solid lines show the nest site/s used by individual pairs of tawny owls. The area measured 2.5X1.5 km.

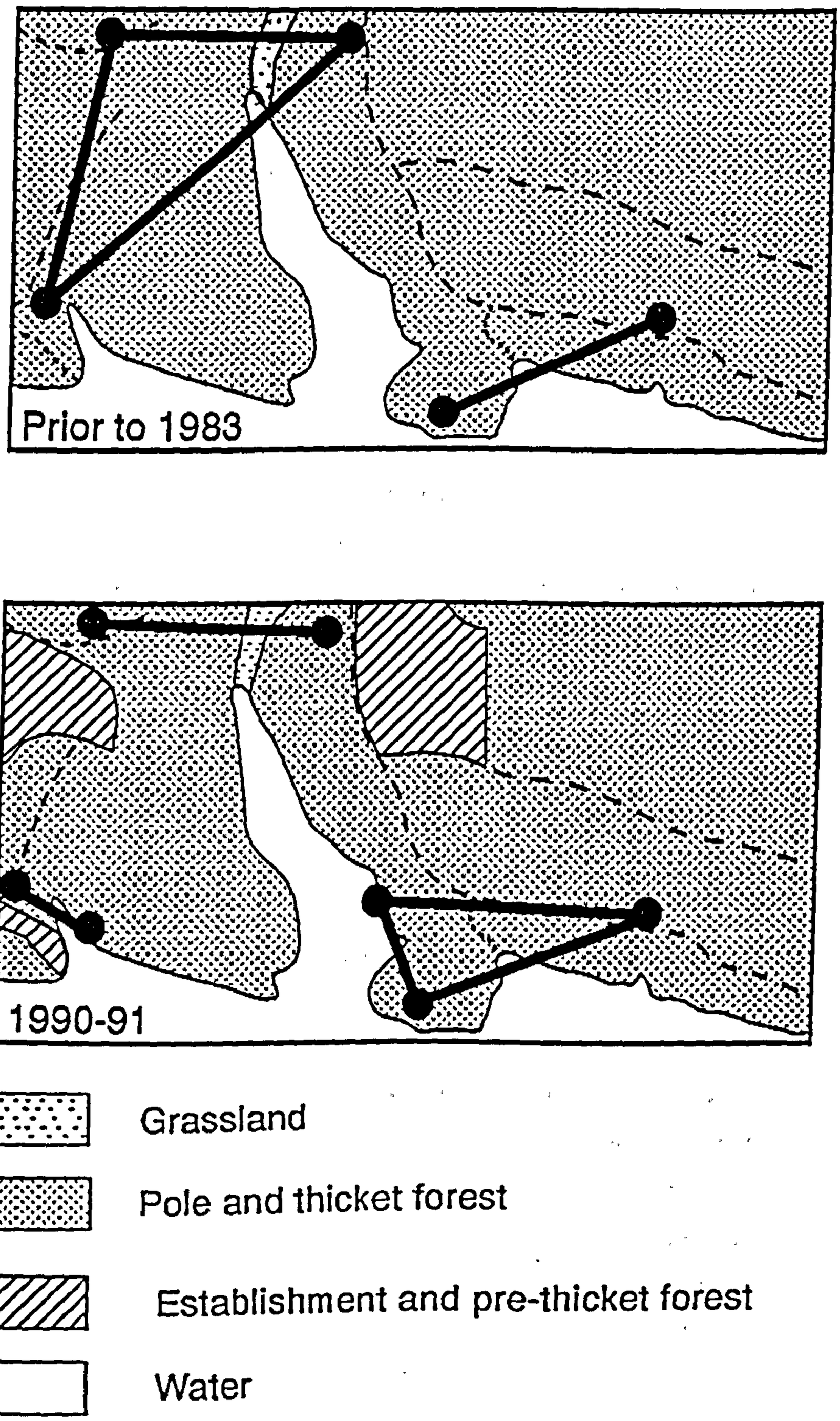


Figure 4.8 The Belling Burn area in the Kielder study area prior to 1983 (upper) and in 1990-91 (lower). The black circles joined by solid lines show the nest site/s used by individual pairs of tawny owls. The area measured 2.5X1.5 km.

No work as been done with tawny owls to test whether nestboxes affect population density. In the present study it was considered unlikely that nestboxes were responsible for the increase in owl density. Forty territories had been located in the Kielder study area prior to the erection of nestboxes in the 1979/80 winter. The subsequent increase to 66 occupied territories in 1991 appeared to be related to patchy clear-felling, producing more vole-rich habitats, and so improving the forest for tawny owls. This was especially evident from comparisons of parts of the Kielder study area where much clear-felling occurred (Figure 4.7) with other parts where there was less (Figure 4.8). It was unlikely that tawny owl populations were limited by the lack of nest sites in either study area prior to the start of the study because of the abundance of disused stick nests, crag sites (Glenbranter) and potential ground sites (usually at the base of a tree).

Southern (1970) was also confident that the provision of nestboxes in his study was not responsible for the number of territories increasing from 20 to 32 during the 10 years when boxes were available. Southern attributed the increase solely to recovery from the severe winter of 1946/47, but provided no evidence to substantiate this.

In both Kielder and Glenbranter almost the whole of the local tawny owl population switched quickly from natural sites to nestboxes. This suggests that boxes were superior to the sites previously used. Owls breeding in stick nests could have been susceptible to predation from larger raptors. Buzzards *Buteo buteo* were present at high density in Glenbranter and goshawks *Accipiter gentilis* at low density in Kielder. Ground nests were vulnerable from these two raptors and also from mammalian predators. Foxes *Vulpes vulpes* occurred in both study areas and wildcat *Felix sylvestris* in Glenbranter. Stick nests, particularly those of crows built high in the crowns of conifers, were also exposed to severe weather. Even

some of the best tree holes were often damp inside. In comparison nestboxes provided a dry and safe environment.

Southern (1970) gave details of the number of nestboxes and the number of pairs of owls using them in his study. In 1950, 2.15 boxes/territory were available, and this had declined to 0.91 boxes/territory by 1959. Overall 55.6% of the nests were in boxes, with no increase in nestbox use during the study. In the first five years 58.6% of nests were in boxes, compared to 52% in the last five years. The reluctance of just under half the population to use nestboxes may have been because the tree holes were good compared to those available in my study areas.

In broadleaved woodland nestboxes are regularly used by both sexes of tawny owls in the winter for roosting. Tawny owls have been recorded roosting in boxes in Wytham Wood, the study area used by Southern (Hirons pers.comm.), in oak *Quercus* spp. forests in Belgium (Delmée *et al.* 1978) and in oak and beech *Fagus sylvaticus* forests in France (Baudvin 1991; Baudvin and Dessolin in press; Baudvin pers.comm.). Delmée *et al.*(1978) also showed that in broadleaved woodland the male will often roost in a box near to the nest.

In contrast, tawny owls in coniferous forests do not appear to roost in nestboxes outside the breeding season. Nest boxes were checked during the winter in both Kielder and Glenbranter. Owls were never found there, and there were never any signs on the box to suggest they were ever used. If they had been, then traces of down and small body feathers would have been present around the entrance hole. Saurola (pers.comm.) also found that nestboxes were not used for roosting during the winter in Finland where the temperatures were much lower. Probably coniferous forests offer sheltered roosting places for tawny owls, whereas broadleaved woodland in winter offers few sheltered roosting sites apart from tree cavities (or nestboxes). In Kielder, nestboxes were also

placed in pairs in a number of territories, in the hope of catching the male roosting in one during the breeding season. This technique had been used successfully by Delmée *et al.*(1978), but in Kielder males were never found roosting in the second box.

4.4.2 Distribution and density of territories

Altitude appeared to have a similar significant influence on the distribution of tawny owls in both study areas, with nesting territories being closer together on the lower ground. Newton *et al.* (1977) found a similar relationship in sparrowhawk, with NND increasing with elevation. In both my study areas, nesting territories were distributed along all the major valleys. This distribution may have resulted from much of the suitable nesting habitat (pole-stage crops) being located on the lower ground. However, tawny owls appeared to avoid nesting on the higher ground, such as watersheds between valley systems where suitable habitats (and nestboxes) were available. A similar type of distribution on the lower and wetter ground has been noted in Switzerland (Eiberle 1970), Finland (Lahti and Mikkola 1974; Lundberg 1980) and elsewhere (Mikkola 1983; Cramp 1985). Eiberle (1970) suggested that this preference for the lower ground was related to prey abundance. This may well be so in my study areas too. In Kielder, the soil types differed between the valley bottoms/sides with surface water gleys, and the upper slopes and watersheds with peaty gleys and blanket peats (Chapter 2). Felled areas on the former sites developed a predominantly grassy vegetation favoured by the tawny owl's most important prey, the field vole (Chapter 3), while on the latter sites heather *Calluna vulgaris* and relatively unpalatable grasses such as *Molinia caerulea* occurred with lower field vole densities. The situation was similar in Glenbranter with grassy vegetation on lower restocked sites and more ericaceous vegetation on higher sites.

Presumably there are also energetic advantages for tawny owls in nesting in sheltered valleys. Most prey are relatively small (less

than 50 g), so during the breeding season, and particularly during the nestling stage, many journeys are made between the nest and foraging areas. The tawny owl is not designed for soaring flight, so it must be far easier to glide downhill with prey and fly back unladen, than the reverse.

Southern (1970) and Hirons (1985b) determined the size of tawny owl territories by plotting the position of calling males and their interaction with neighbours over repeated visits. I used a different method based on the nearest neighbour distance between pairs (section 4.2.2). Therefore caution is needed when comparing territory size between studies (Table 4.9). Mean territory size of 48 ha in Kielder was close to that found in the Forest of Ae, Dumfries in similar habitat to Kielder (Hirons 1985b). The smallest territories so far recorded in Britain were those in Wytham Wood, Oxfordshire, with an average size of 18.2 ha (Table 4.9).

Southern (1970) further separated territories into those in closed woodland and those with woodland and open ground. The average size in the former habitat was 12.1 ha and in the latter 20.2 ha. This was because tawny owls fed largely on wood mice *Apodemus sylvaticus* and bank vole *Clethrionomys glareolus* which were both more abundant in wooded than in open habitats. In my study the opposite applied; field voles were the main prey and these were most abundant in open grassy areas. So owl density increased as clear-felling created a patchwork of foraging (establishment and pre-thicket crops) and roosting/breeding areas (pole-stage crops). Continuous areas of closed-canopy spruce forest held a very low density of tawny owls.

4.4.3 Occupancy of territories

Unoccupied territories were present every year in both my study areas. This apparently did not occur in long-term studies of tawny owls in broadleaved woodland (Southern 1970; Delmée *et al.* 1978). In Glenbranter the percentage of unoccupied territories was significantly lower and showed far less variation than in Kielder

Table 4.9 Tawny owl territory size from studies of 10 or more pairs in Britain and Europe.

Habitat	Area (ha)	SE	n	Reference
Britain				
Mainly broadleaved woodland, Oxfordshire. Same study area used by Southern (1970)	18.2	0.38	31	Hirons (1985b)
Farmland, small copses and hedgerows (all broadleaved), Warwickshire	37.4	4.43	10	Hirons (1985b)
Mature spruce plantation, Dumfries	46.1	1.72	17	Hirons (1985b)
Spruce forest, Northumberland	48.2	4.33	69	This study
Spruce forest, Argyll	69.8	6.47	58	This study
Europe				
Oak woodland, Belgium	65-75	-	10	Delmée *et al.*(1978)
Urban areas, Italy	13-20	-	19-20	Galeotti (1990)
Mixed farmland, Italy	11.2	-	14	Cesaris (1968)

(Table 4.5). In Kielder occupancy was related to vole year classes, with significantly fewer territories occupied in low vole years than in increasing or declining vole years (Table 4.6). In the latter two vole year classes, 90-91% of territories were occupied, which was similar to Glenbranter (90.9-96.6%). The low vole years in Kielder followed winters when vole populations were at their lowest in the three-year cycle (Chapter 3) and the more varied occupancy resulted from increased mortality of adult owls (Chapter 6). In Kielder and Glenbranter, the presence of unoccupied territories each year and the continuing increase in the number of occupied territories suggests that the population could be higher in both study areas but may currently be limited by a lack of owls

at certain phases in the three-year vole cycle. This aspect is explored further in Chapter 8.

In conclusion, in both study areas nest sites did not limit tawny owl populations either before or after the erection of nestboxes. Nesting territories were regularly distributed along the lower valleys with the spacing between nesting territories influenced by elevation. The number of nesting territories increased during the study, apparently due to habitat fragmentation which resulted in more food available for tawny owls.

4.5 Summary

1. Prior to the erection of nestboxes tawny owls used a wide variety of nest sites in both study areas, including tree cavities, crags and ground nests, man-made structures and stick nests of other species.

2. In Kielder, 83% of the breeding population switched to using nestboxes in the first year they were available. All pairs were using nestboxes by the fourth year. A similar pattern occurred in Glenbranter. There was always a surplus of nestboxes in each study area/year.

3. Forty territories were located in the Kielder study area prior to 1979 when the first nestboxes were erected. The number of occupied territories increased in Kielder from 44 in 1981 to 66 in 1991, and in Glenbranter from 23 in 1984 to 56 in 1991. After controlling for slight extensions to each study area the net increase in occupied territories amounted to 4.5% per annum in Kielder and 13.9% per annum in Glenbranter.

4. The increase in the population of owls in both study areas was attributed to the improvement of habitat caused by clear-felling which resulted in more food (field voles in particular) for tawny owls.

5. There were unoccupied territories each year in both study areas. On average there were significantly more unoccupied territories in Kielder (12%) per year than in Glenbranter (7%). There were also lower annual fluctuations in the proportion of unoccupied territories in Glenbranter (range 3.4-9.1%) than Kielder (range 5.9-22.0%).

6. In Kielder occupancy rates were significantly related to vole abundance, with lower territory occupancy in low vole years (81%) than increasing and decreasing vole years (90-91%).

7. Tawny owl nesting territories were evenly distributed along the lower valleys in each study area. In Glenbranter most nesting territories were below 100 m altitude (median 70 m), whereas in Kielder most were above 200 m (median 220 m).

8. Nearest neighbour distances between nesting territories in the last year of the study (1991) were significantly closer in Kielder (median 0.74 km) than Glenbranter (median 0.84 km) resulting in median territory sizes of 43 ha in Kielder and 55 ha in Glenbranter.

9. There was a significant relationship ($P<0.001$) between NND and altitude after controlling for differences in altitude between the two study areas.

CHAPTER 5
REPRODUCTION

5.1 Introduction

When moorland is converted into forest, field vole *Microtus agrestis* populations increase dramatically after planting and show peaks in numbers every three to five years (Chitty 1952; Charles 1956; Charles 1981). This abundant food resource promotes increased density and productivity of those nocturnal and diurnal birds of prey able to exploit it, notably short-eared owl *Asio flammeus* (Goddard 1935; Lockie 1955; Village 1987), long-eared owl *Asio otus* (Village 1981), kestrel *Falco tinnunculus* (Village 1982; Village 1990) and barn owl *Tyto alba* (Shawyer 1987; Shaw and Dowell 1990; Taylor *et al.* 1992). Canopy closure occurs soon after the trees are fifteen years of age, leading to a loss of the luxuriant ground vegetation, and a dramatic reduction in both field vole numbers and the predators dependent upon them.

Conditions suitable for field voles are again created at the end of each rotation, when trees are clear-felled allowing a dense ground vegetation to develop during the establishment of the next conifer crop (Chapters 2 and 3). However, prior to the present study, there had been no attempt to investigate how field vole populations are exploited by raptors at this stage in the forest cycle, despite the fact that restocking will occur at the end of every rotation, while afforestation occurs only once.

The tawny owl *Strix aluco* colonizes spruce forests during the first rotation but its reproduction has not been studied in this novel habitat. Considering just how abundant the tawny owl is both in Britain and Europe, there is a dearth of studies on its reproduction in other habitats too, compared for instance to the vast literature on diet (Mikkola 1983; Cramp 1985). Only three studies have investigated the reproduction and food supply of tawny owls in Britain. Two were in lowland broadleaved woodland near Oxford where bank voles *Clethrionomys glareolus* and wood mice *Apodemus sylvaticus* were the main prey (Southern 1970; Hirons

1976), and the third was on farmland in Aberdeenshire where field voles were important (Hardy 1977). Percival (1990) has recently analysed extensive data from the National Ringing Scheme and Nest Record Scheme of the British Trust for Ornithology on tawny and barn owls and related these to various environmental parameters.

Other long-term studies on tawny owls have been undertaken in Europe. Delmée *et al.* (1978) studied owls in ten territories over 15 years in Belgium; Wendland (1984) presented data from 17-20 pairs over a 20-year period from forests in Berlin; Linkola and Myllymäki (1969) presented a large amount of data from Finland; while Wallin (1988) provided a detailed account of life history evolution and ecology of tawny owls from over 200 territories in SW Sweden.

Increasing daylength acts in a proximate way to trigger breeding in raptors (Newton 1979) as in many other birds (Lack 1954), but within individual species an array of other proximate factors can act to fine-tune the start of breeding and reproductive output. Of these factors, food supply is probably one of the most important for raptors (Newton 1979; Drent and Daan 1980; Korte and Wattel 1988; Meijer *et al.* 1989; Hörnfeldt and Eklund 1990). In addition, age and experience (Newton *et al.* 1981; Pietiäinen 1988a) and habitat quality may also influence the date of laying (Newton 1991) and may act through food-supply. Food-supply is also a major factor influencing clutch size and nest success of raptors (Newton 1979). In this Chapter, I explore how some of these proximate factors affect reproductive performance in tawny owls in the Kielder and Glenbranter study areas (Chapter 2).

5.2 Methods

5.2.1 Visits to nests

Visits to potential nest sites (nestboxes and natural sites) commenced during the first vole assessment in March, with subsequent visits timed to obtain the data required with the

minimum of disturbance. A nesting territory was considered to be occupied when a fresh scrape, with down and/or small body feathers, was found in at least one nest site during the last two weeks of March and the first two weeks of April (Chapter 4).

5.2.2 Timing of breeding

Different studies have used different measures of the start of breeding. The most common are: (a) the date when the first egg was laid, and (b) the date when incubation commenced. I used the latter measure as did Southern (1970) because nest visits during the laying period were avoided to minimise the risk of desertion. Therefore, the exact date when the first egg was laid was unknown. Tawny owls appear to lay eggs at about two-day intervals after the second egg (Mikkola 1983), but the interval between the first and second egg can be more variable at two-four days or more (Southern 1970; Petty unpublished data). Females usually stay at the nest as soon as the first egg is laid, but when flushed, single eggs are invariably cold, suggesting that they are not properly incubated. Once two eggs are present, they are usually warm when the nest is visited. This suggests that incubation often commences with the second egg.

I calculated the date of the start of incubation (SIC) by adding the age (in days) of the largest chick in the brood (when <15 d old) estimated from winglength growth measurements (Petty unpublished data) to an incubation period of 30 d and subtracting the sum from the date when the chick was measured. Southern (1970) gives a mean incubation period of 29.7 d compared to 28-29 d by Mikkola (1983) and 28-30 d by Cramp (1985). SIC was expressed as a numerical value in days with 1 March = 1, 2 March = 2, 1 April = 32 etc. The date when the first egg was laid can be estimated by SIC-2. This makes two additional assumptions; that incubation does start with the second egg laid, and that the laying interval between the first and second egg is two days. It will therefore be

less accurate than SIC, so throughout this chapter SIC is used instead of the date when the first egg was laid.

5.2.3 Clutch size and egg measurements

On the first visit to a nest with eggs, each egg was marked with a unique code using a black spirit-based felt-tip pen. FC 1/90, FC 2/90 etc. denotes the first and second eggs marked in 1990. The length (l) and breadth (b) (at the widest point) were measured to the nearest 0.01 cm with metal vernier calipers or plastic dial calipers. Each egg was weighed (w) in a small polythene bag with a 50 g pesola balance, to the nearest 0.1 g. A density index (DI) was calculated for each egg when $DI = W/(0.507*b^2*l)$. The DI decreases through incubation as the egg loses weight. In a comparative study Furness and Furness (1981) found that the shape of the curve depicting this decline in density, plotted against days to hatching, was similar over a wide range of species and genera. Using this relationship, it was possible to calculate both laying and hatching dates for tawny owl eggs examined at any stage of incubation (Figure 5.1). Any clutch with a DI for any egg >1.060 could have been incomplete, so was revisited to obtain the complete clutch. Clutches where all eggs had a DI <1.059 were complete.

5.2.4 Brood size

The number of chicks hatching was determined from clutch size minus any unhatched eggs. There were no instances of eggs "disappearing", either from a deserted or a fully incubated clutch, so it was reasonable to assume that all eggs hatched unless they were still in the nest. Pesticide contamination has been implicated in egg loss in other raptors (Newton 1979). However, shell thinning due to high DDE levels in the adults can be discounted, as DDE levels were very low and shell indices were normal in eggs analysed from both study areas (Petty, unpublished data). There were no predators in either study area, such as pine marten *Martes martes*, that could remove eggs or chicks from active owl nests in boxes or elevated natural sites. Foxes *Vulpes vulpes* were potential predators of

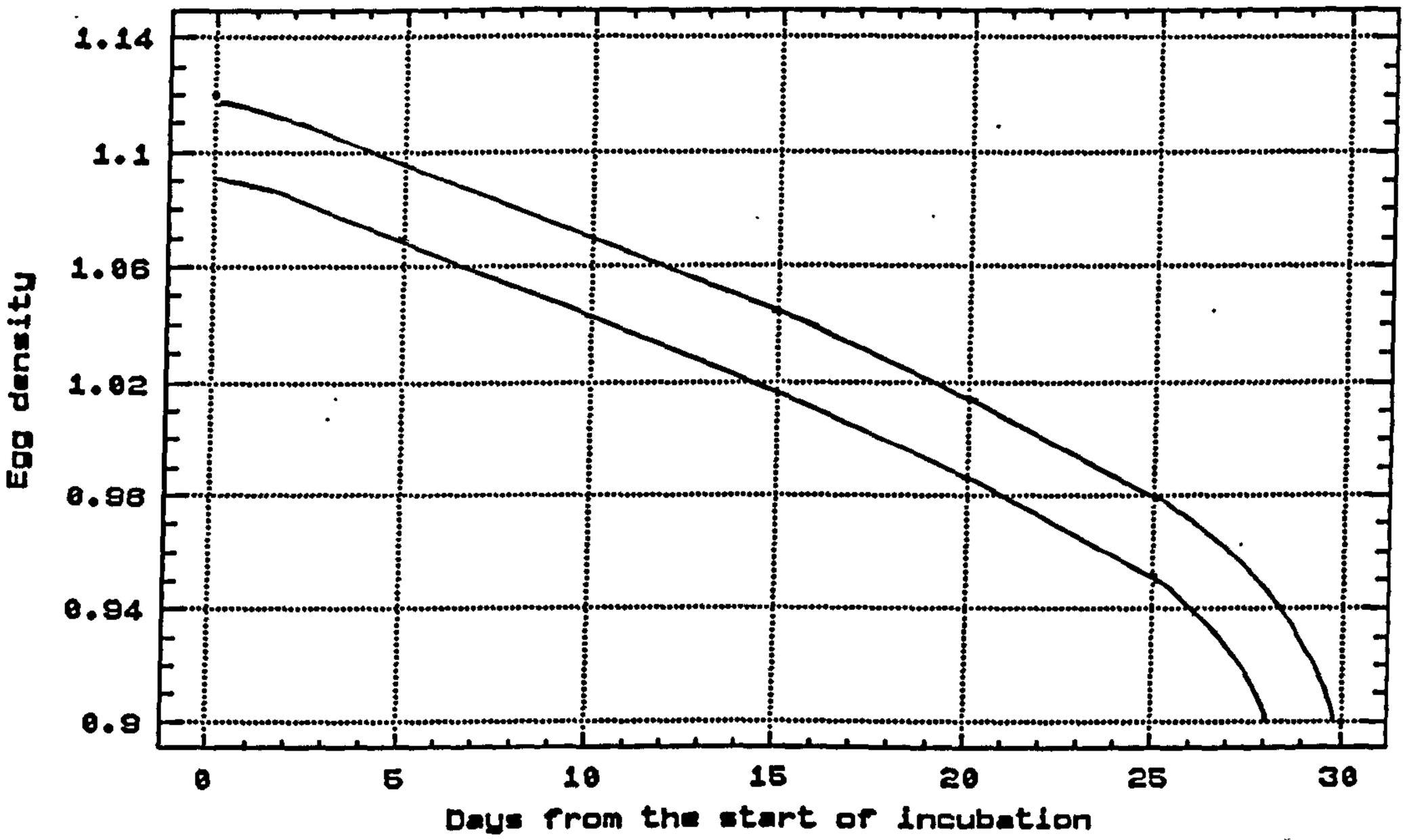


Figure 5.1 Graph showing the decline in egg density during incubation. This uses the curve described by Furness and Furness (1981), adapted for the incubation period (X) and the range of egg densities in tawny owls (Y). The lines show the range of egg densities at any point during incubation. Hatching date was predicted assuming a mid-range density. See text (5.2.3) for calculating egg density.

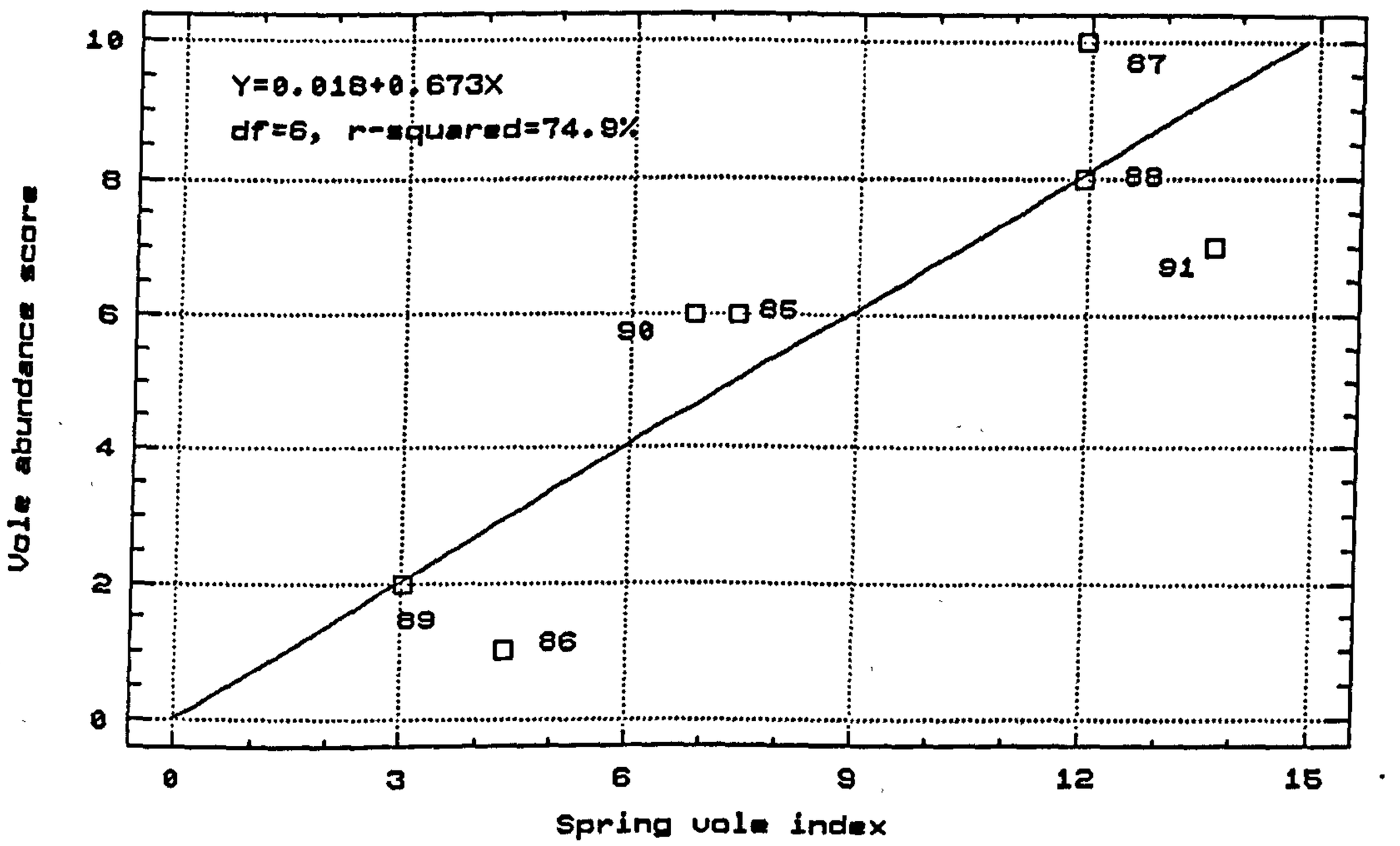


Figure 5.2 Relationship between the vole abundance score and the mean spring vole index in Kielder 1985-91 (Table 5.2).

ground nests, but few such nests were found once nestboxes were provided (Chapter 4). Red squirrels *Sciurus vulgaris*, but not grey squirrels *S.carolinensis*, were present in both study areas, and were considered capable of removing eggs from deserted nests but this was never recorded. Squirrels regularly occupied nestboxes not used by owls (Chapter 4) and occasionally built dreys on top of deserted owl eggs, but the eggs were unbroken.

Chicks were ringed after they reached 150 g (9-10 days old) and nests were revisited in the last week of the nestling period to count and remeasure chicks. The number of chicks fledging (leaving the nest) was taken as the number recorded on the last visit prior to fledging minus the remains of any dead chicks in the nest after fledging. Dead chicks were identified from their ring number. From a sample of nests visited regularly up to fledging, there was no evidence of a dead chick or its remains being completely removed from the box by the adults once it had been ringed. The body either rotted intact in the box or was partly eaten by the female or remaining chicks. Sometimes all that remained was a leg and ring and occasionally just the ring, but there were always feathers from the dead chick in the box, particularly the developing remiges and rectrices.

5.2.5 Desertions due to observer disturbance

Some tawny owls deserted the nest following observer visits and/or catching adults. In Kielder this amounted to 50 (12.8%) of the 391 nests where at least one egg was laid (Table 5.1). The relatively high desertion rates in the earlier part of the study (1981-1983) were reduced as experience was gained. Desertions increased again in 1988 with the development of a technique for catching males (Chapter 6). In Glenbranter, 29 (14.1%) clutches out of 205 were deserted following observer disturbance.

Table 5.1 Number of desertions associated with observer visits to nests of tawny owls at different stages in Kielder and Glenbranter. Some pairs relaid (a) while others did not (b).

Year	Clutches* (n)	Number of clutches deserted (a+b)							
		laying		incubation		chicks		total	
		a	b	a	b	a	b	a	b
Kielder									
80	19	1	0	0	3	0	0	1	3
81	50	1	0	6	2	2	1	9	3
82	40	4	0	2	1	0	0	6	1
83	11	1	0	0	1	0	0	1	1
84	43	0	0	0	1	0	0	0	1
85	45	1	0	0	1	0	0	1	1
86	4	0	0	0	0	0	0	0	0
87	55	6	0	0	0	1	0	7	0
88	55	2	0	2	2	1	4	5	6
89	14	0	0	0	0	0	0	0	0
90	55	3	0	1	0	0	0	4	0
80-90	391	19	0	11	11	4	5	34	16
Glenbranter									
84	21	0	0	1	0	0	0	1	0
85	20	0	0	0	4	0	0	0	4
86	19	1	0	2	0	0	0	3	0
87	34	3	0	2	0	0	1	5	1
88	33	1	0	1	2	0	1	2	3
89	32	1	0	1	3	0	1	2	4
90	46	0	0	1	2	0	1	1	3
84-90	205	6	0	8	11	0	4	14	15

** Includes first and second clutches and clutches that were deserted during the laying period*

Most desertions followed the first visit to the nest, when the eggs were marked or the female caught. It was evident from the condition of the eggs on the subsequent visits that the female never returned to the nest, as the numbers on the eggs fade during incubation. Observer disturbance was considered the primary cause of such desertions because many of the females moved to another site and relaid. This would have been unlikely if food shortage had been the causal factor.

Desertions happened during egg-laying (38% in Kielder and 21% in Glenbranter) when only one or two eggs had been laid, during incubation (44% in Kielder and 66% in Glenbranter), or during the nestling period (18% in Kielder and 14% in Glenbranter) (Table 5.1). Desertion during egg-laying always resulted in the clutch being continued (Table 5.1) without interruption at another nest site within the territory. Of the females which deserted after incubation commenced, about half (50% in Kielder and 42% in Glenbranter) laid a second clutch at a new nest site, but after an interval much longer than the normal between eggs (section 5.3.3.6). Second clutches were also recorded after females deserted young chicks, with four instances in Kielder and none in Glenbranter (Table 5.1). Generally the more advanced the nesting cycle when the failure occurred, the less the chance of a relay. Pairs which failed with chicks older than six days never relaid.

Virtually all repeat clutches were considered to result from first-clutch desertions caused by the observer. Therefore to avoid using two or more clutches from the same female in a year, the procedures below aimed to remove these observer effects from most of the analysis in this chapter.

A. Incompleted (unincubated) clutches of one or two eggs that were deserted were excluded and substituted by the replacement clutch with its brood size and start of incubation.

B. Completed (incubated) first clutches that were deserted were substituted by the clutch and brood size from the replacement clutch, but the start of incubation from the first clutch was used. There was no significant difference between initial and repeat clutch sizes (section 5.3.3.6).

C. When deserted first clutches were not replaced, or when these were replaced and subsequently failed, then clutch size and start of incubation from the first clutch was used, but all other data such as brood size were excluded, provided the

desertion was considered to have been caused by observer disturbance. This resulted in unequal sample size in most data sets.

5.2.6 Field vole abundance

Field voles were the most important food of tawny owls (Chapter 3). Two methods were used to assess the abundance of voles. First, a subjective score was made in Kielder, during the period when tawny owls were breeding (March-May) (Table 5.2). This indicates that since 1981, there have been three, 3-year cycles of vole abundance. The years of peak abundance were 1981, 1984, 1987 and 1990. In the latter year the vole population was much slower to increase after the low in 1989, compared to the two previous low years of 1983 and 1986 when voles were much more abundant by late summer. Second, vole abundance was measured by both trapping and vole sign indices in each study area from summer 1984 to summer 1990 (Chapter 3). The vole abundance indices used in this chapter were the mean PTIs from Chapter 3, Table 3.13. This index was based on fresh grass clippings in vole runs in the vole sign index areas. The reliability of the subjective score can be checked by comparing it to the mean spring vole index for 1985 to 1991. There was a significant relationship between the two methods ($r_s=0.84$, $n=7$, $P<0.05$) (Figure 5.2), giving confidence that the vole scores did reflect spring vole abundance. Vole population levels were not synchronised in the two study areas (Chapter 3, Figure 3.14).

5.2.7 Meteorological data

The meteorological data used in this chapter were taken from the *Monthly Weather Report* published by the Meteorological Office, and referred to Kielder Castle, near the centre of the Kielder study area, and Benmore (Younger Botanical Garden) at the southern end of the Glenbranter study area (Chapter 2). Five monthly weather data were used, namely;

A. Mean daily temperature (degrees celsius)

B. Total rainfall (mm)

Table 5.2 Vole population score for Kielder, 1981-1991.

Year	Vole score+	Vole pop trend*	Description of vole population
81	8	I	Moderate over winter and increasing during year
82	5	D	High in winter and decreasing from spring onwards
83	2	L	Low in winter and spring, increasing late summer
84	8	I	High over winter and remaining high throughout year
85	6	D	High over winter and decreasing from spring onwards
86	1	L	Very low over winter and spring, increasing by late summer
87	10	I	High over winter and remaining high throughout year
88	8	D	High over winter and decreasing from spring onwards
89	2	L	Low in winter and spring, increasing by late autumn
90	6	I	Moderate over winter increasing through year
91	7	D	High over winter and decreasing from summer onwards

**Vole population trend, I = increasing vole population, D = declining vole population, L = low population. Refers to the vole population level during March-June period.*

+Subjective index assessed during the March-May period with 10 = the highest vole population and 0 = the lowest vole population.

The index was based on the amount of vole signs (droppings, grass clippings, runways) in open habitats with grassy vegetation.

C. Number of days with 1.0 mm or more rain

D. Number of days with snow lying at 09.00 hrs.

E. Number of days with air frosts

5.2.8 Biometrics from adult owls

Two measurements were taken from adult owls. Mass was measured to the nearest 2 g with a 500 g or 1000 g Pesola balance. Winglength was taken by the maxiumm chord method (Spencer 1984) to the nearest 1 mm using a 300 mm winglength ruler supplied by the British Trust for Ornithology. Most adult owls were caught for measurement during the early nestling period, when the youngest chick in a brood was 5-10 days old as this minimized the risk of adults deserting (Chapter 6, section 6.2.4). Biometric data were available for females for the whole of the study, but for males from only 1988-1990. Some females were caught more than once each year when they were reweighed but only the first mass measurement each year was used. Weights from the same female but in different years were treated as independent data.

5.3 Results

Data on reproduction were collected in Kielder during 1979-1990 (1991 for some data) and Glenbranter during 1983-1990 (1991 for some data). Sample sizes from 1979 in Kielder and 1983 in Glenbranter were small and may not have been representative, so for most analyses they were excluded. Where comparisons were made between study areas, then data from the years 1984-1990 (1984-91 in some data sets) were used. When exploring relationships between vole abundance and reproductive performance, data from both study areas was first used to see if vole abundance had a similar influence independent of study area. If not, then data from Glenbranter were excluded and the correlations or regressions recalculated for Kielder only. Because some vole assessments were missed in Glenbranter (Chapter 3) there were sometimes not enough data points to calculate separate relationships for this area. Vole

numbers did not fluctuate in parallel in both study areas (Chapter 3, Figure 3.14).

5.3.1 Proportion of the population breeding

Overall, a significantly higher proportion of pairs bred (laid at least one egg) in occupied territories in Glenbranter (79%) than in Kielder (72%) (1984-1991, chi-squared with Yates correction = 4.34, df=1, P<0.05) (Table 5.3). There was also considerable difference between study areas in the between-year variation in the proportion of pairs laying. A more consistent proportion laid each year in Glenbranter, ranging from 58.8% (1989) to 89.3% (1991). In Kielder there was far greater variability, with a small proportion of the population laying in the low vole years of 1983 (28.2%), 1986 (8.2%) and 1989 (26.9%), but 69-96% in other years.

To investigate the relationship between vole abundance and the incidence of breeding, the vole indices from the previous autumn, winter (autumn+spring/2) and current spring were individually plotted against the proportion of pairs which laid each year (1985-1991. The best linear relationship was with the previous autumns vole index (Figure 5.3). This explained 51.2% (P<0.05) of the variability in the proportion of pairs breeding, the winter vole index explained 46.8% (P<0.05) of the variability and spring index only 17.6% (NS). The relationship between the proportion of pairs laying and vole abundance changed little when the three data points from Glenbranter were excluded (Kielder only Y=16.56+5.42X, df=6, r-squared = 58.2%).

The proportion of pairs laying may also have been influenced by meteorological factors. Autumn vole abundance appeared to be important for conditioning tawny owls for breeding. Favourable weather at this time may have been important too. The five weather data for autumn (September-November) were initially used in a correlation analysis with the proportion of pairs laying (Table 5.4). The only significant relationship (r=-0.758, P<0.01) was with

Table 5.3 Annual reproductive performance of occupied tawny owl territories in Kielder and Glenbranter.

Year	Occupied territories (A)	Pairs not laying (% of A) (B)	Pairs laying (% of A) (C)	Pairs failing due to observer disturbance (D)	Pairs failing naturally		Successful pairs (% of C-D)
					with eggs (% of C-D) (E)	with chicks (% of C-D) (F)	
Kielder							
80	26	8(30.8)	18(69.2)	3	1 (6.7)	1 (6.7)	13 (86.7)
81	44	3 (6.8)	41(93.2)	3	2 (5.3)	3 (7.9)	33 (86.8)
82	42	6(14.3)	36(87.7)	1	2 (5.7)	1 (2.9)	32 (91.4)
83	39	28(71.8)	11(28.2)	2	1(11.1)	0 (0.0)	8 (88.9)
84	46	3 (6.5)	43(93.5)	1	2 (4.8)	0 (0.0)	40 (95.2)
85	50	6(12.0)	44(88.0)	1	2 (4.7)	2 (4.7)	39 (90.7)
86	49	45(91.8)	4 (8.2)	0	0 (0.0)	0 (0.0)	4(100.0)
87	56	8(14.3)	48(85.7)	0	2 (4.2)	1 (2.1)	45 (93.7)
88	61	11(18.0)	50(82.0)	6	0 (0.0)	4 (9.1)	40 (90.9)
89	52	38(73.1)	14(26.9)	0	0 (0.0)	2(14.3)	12 (85.7)
90	64	10(15.6)	54(84.4)	1	3 (5.7)	0 (0.0)	50 (94.3)
91	66	3 (4.5)	63(95.5)	2	5 (8.2)	0 (0.0)	56 (91.8)
80-91	595	169(28.4)	426(71.6)	20	20 (4.9)	14 (3.5)	372 (91.6)
84-91	444	124(27.9)	320(72.1)	11	14 (4.5)	9 (2.9)	286 (92.6)
Glenbranter							
84	23	3(13.0)	20(87.0)	0	2(10.0)	2(10.0)	16 (80.0)
85	25	5(20.0)	20(80.0)	5	0 (0.0)	1 (6.7)	14 (93.3)
86	28	11(39.3)	17(60.7)	1	0 (0.0)	3(18.7)	13 (81.3)
87	35	5(14.3)	30(85.7)	2	0 (0.0)	2 (7.1)	26 (92.9)
88	40	8(20.0)	32(80.0)	4	1 (3.6)	8(28.5)	19 (67.9)
89	51	21(41.2)	30(58.8)	4	5(19.2)	7(26.9)	14 (53.9)
90	52	6(11.5)	46(88.5)	2	3 (6.8)	5(11.4)	36 (81.8)
91	56	6(10.7)	50(89.3)	0	5(10.0)	4 (8.0)	41 (82.0)
84-91	310	65(21.0)	245(79.0)	18	16 (7.0)	32(14.1)	179(78.9)

"Pairs laying" = where at least one egg was laid. "Successful pairs" = where at least one chick fledged

Table 5.4 Relationships [r(n)P] between five weather variables in autumn and winter and three reproductive variables from tawny owls. Each data represented one study area/year (Kielder 1980-1990 and Glenbranter 1984-1990). Sample sizes are variable because weather data were not available for some seasons.

Season and weather variable	% of pairs laying	Start of incubation	Clutch size
Autumn (Sept-Nov)			
1	0.560(11)NS	-0.008(13)NS	-0.316(13)NS
2	0.276(15)NS	0.123(17)NS	-0.388(17)NS
3	0.302(15)NS	-0.057(17)NS	-0.278(17)NS
4	-0.499(14)NS	0.409(17)NS	-0.394(17)NS
5	-0.758(13)**	0.228(15)NS	0.091(15)NS
Winter (Dec-Feb)			
1	0.025(14)NS	0.223(14)NS	-0.312(15)NS
2	0.154(17)NS	0.100(19)NS	-0.189(19)NS
3	0.021(17)NS	-0.024(19)NS	-0.093(19)NS
4	0.136(16)NS	-0.436(17)NS	0.346(18)NS
5	0.004(15)NS	-0.277(17)NS	0.493(17)*

Weather variables; 1 = mean daily temperature (degrees celsius), 2 = total rainfall (mm), 3 = number of days with 1.0 mm or more of rain, 4 = number of days with snow lying at 09.00 hrs., 5 = number of days with air frost.

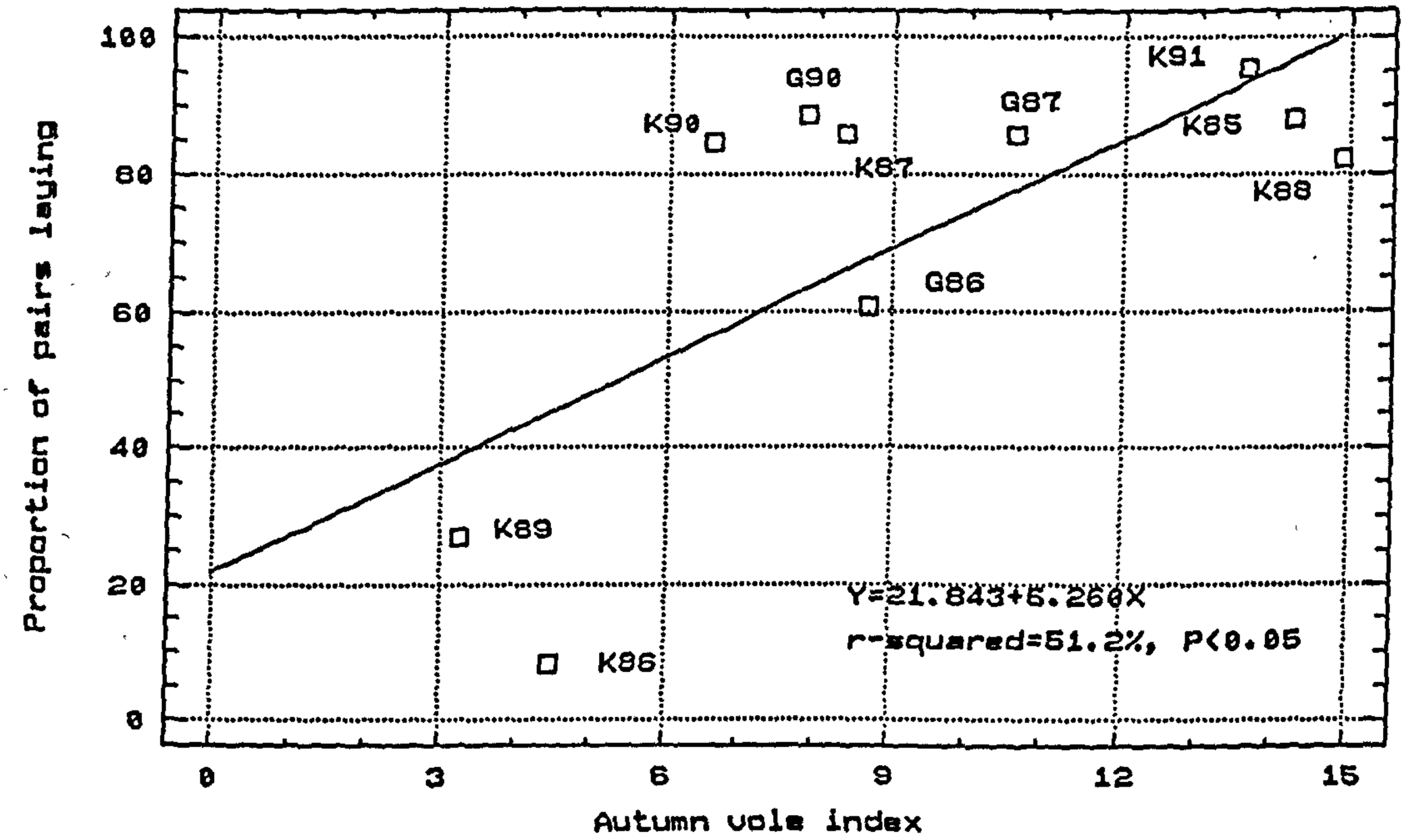


Figure 5.3 Relationship between the proportion of tawny owl pairs breeding and the previous autumns mean vole index. Each point relates to a study/area year, K = Kielder and G = Glenbranter.

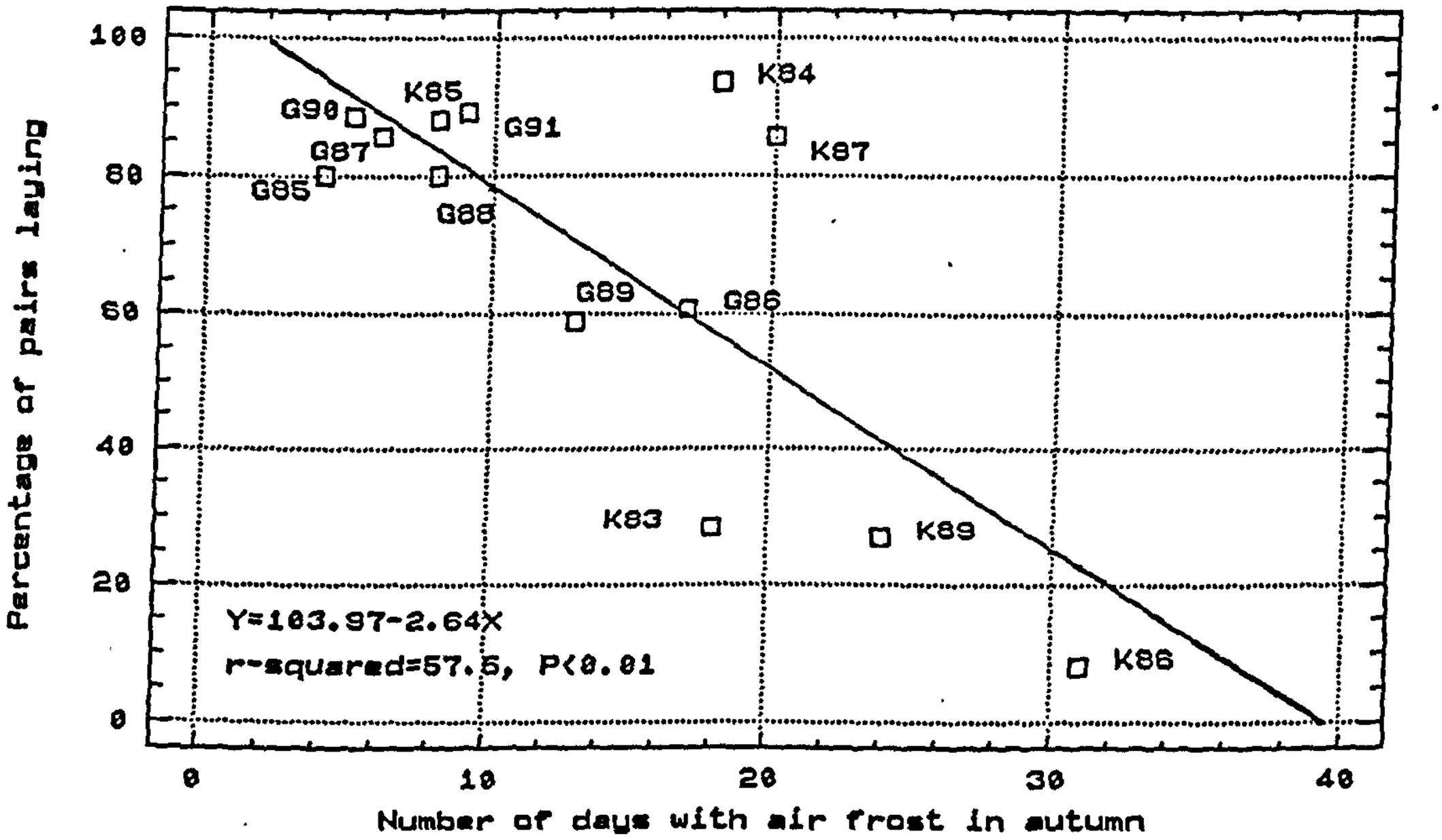


Figure 5.4 Relationship between the proportion of tawny owl pairs breeding and the number of days with air frost in the previous autumn. Each point relates to a study/area year, K = Kielder and G = Glenbranter.

number of days with air frost which explained 57% of the variation in the proportion of pairs laying (Figure 5.4). The correlation coefficients were still high when this analysis was repeated for each area (Glenbranter r=-0.821, n=7, P=0.02; Kielder r=-0.725, n=6, P=0.10) giving confidence that this was not a spurious relationship, although the relationship was not quite significant in Kielder. There were no significant relationships between the percentage of pairs laying and any weather variables during the winter (December-January) (Table 5.4).

To try and clarify the situation, the number of days with air frost in the autumn was entered as the independent variable in a multiple regression model with the proportion of pairs laying as the dependent variable. This explained 53.6% of the variation in the proportion of pairs laying ($F=14.88$, $df=1,12$, $P<0.01$). When the autumn vole index was added to this model, the amount of variation explained increased to 71.8% ($F=8.63$, $df=2,4$, $P<0.05$). Adding an "autumn vole index*number of days with air frost" interaction further increased the amount of variation explained to 85.5%, suggesting that the number of days with air frost may also have influenced vole abundance. The best model was obtained when the autumn vole index was removed ($F=18.58$, $df=2,4$, $P<0.01$, r-squared=85.4%), leaving the number of days with air frost and the interaction term as independent variables (Table 5.5).

5.3.2 Timing of breeding

5.3.2.1 Variation in the timing of breeding between study areas and years

There was a significant difference between study areas in the mean start of incubation (SIC) during the seven years 1984-90 (Mann-Whitney U-test, $Z=8.22$, $P<0.001$) (Table 5.6 and Figure 5.5). There was also significant variation in SIC between years both in Kielder (1980-90 Kruskal-Wallis, test statistic = 123.00, $P<0.001$; 1984-90 test statistic = 84.39, $P<0.001$) and to a lesser extent in Glenbranter (1984-90 Kruskal-Wallis, test statistic = 42.17,

*Table 5.5 A multiple regression model using the number of days with air frost in autumn (AAF) and a autumn vole index (AVI) * number of days with air frost in autumn interaction, explained 85.4% of the variation in the proportion of pairs laying in the following spring (F=18.57, df=2,4, P<0.01).*

Independent variable	Coefficient	SE	t	Significance level
Constant	89.902	12.698	7.086	0.002
AAF	-3.812	0.641	-5.951	0.004
AVI*AAF	0.317	0.133	2.381	0.076

Table 5.6 Mean annual start of incubation (SIC) in tawny owls in Kielder (1980-90) and Glenbranter (1984-90).*

Year	SIC (mean)	n	SE	SD	Range	Mode	Median	SS	SK
Kielder									
80	42.42	17	3.42	14.12	20-69(49)	62	40.0	0.70	-0.24
81	25.39	41	2.17	13.90	2-71(69)	22	23.0	3.71	4.26
82	26.76	34	1.16	9.36	5-40(35)	27	27.5	-1.70	-0.22
83	41.00	10	3.56	11.56	22-65(43)	38	40.5	0.82	1.35
84	15.86	42	1.24	8.00	5-42(37)	15	15.0	3.37	2.60
85	23.75	44	1.68	11.13	4-51(47)	30	22.5	1.42	-0.27
86	44.00	4	4.55	9.09	36-56(20)	36	42.0	0.73	-0.31
87	21.32	47	1.62	11.13	2-63(61)	15	20.0	3.21	4.39
88	18.02	50	1.56	11.06	-3-41(44)	24	18.0	0.31	-1.20
89	41.29	14	3.28	12.28	22-61(39)	45	41.0	0.33	-0.80
90	32.41	51	1.48	10.59	18-66(48)	25	30.0	4.04	2.56
80-90	25.71	354	0.72	13.57	-3-71(74)	15	24.0	5.40	2.58
84-90	23.89	252	0.81	12.90	-3-66(69)	15	23.0	4.45	1.70
Glenbranter									
84	22.15	20	1.88	8.39	5-39(34)	23	22.5	0.25	0.02
85	35.35	20	1.76	7.86	21-51(30)	40	35.5	0.15	-0.16
86	36.19	16	2.96	11.83	17-70(53)	38	35.0	2.55	3.38
87	34.77	30	1.93	10.60	2-55(53)	31	35.5	-1.91	2.36
88	32.90	30	1.68	9.18	14-52(38)	29	30.5	0.40	-0.31
89	39.79	29	1.72	9.28	23-56(33)	38	41.0	-0.39	-1.03
90	30.44	45	1.20	8.03	18-51(33)	30	29.0	1.98	-0.07
84-90	33.07	190	0.75	10.27	2-70(68)	29	32.0	0.91	1.41
Overall	28.28	544	0.56	12.99	-3-71(74)	29	28.0	3.61	1.35

Range = maximum and minimum and the difference in brackets.
SS = Standardized skewness coefficient
SK = Standardized kurtosis coefficient

SS and SK tests for significant deviations from the normal distribution. In large samples the standardized coefficients are approximately 0. When these values lie outside the range -2.0 to +2.0 the data may depart significantly from a normal distribution. Skewness measures how asymmetric the data distribution are while kurtosis reveals how flat or steep they are.

** 1 March = 1, 2 March = 2, 1 April = 32 etc.*

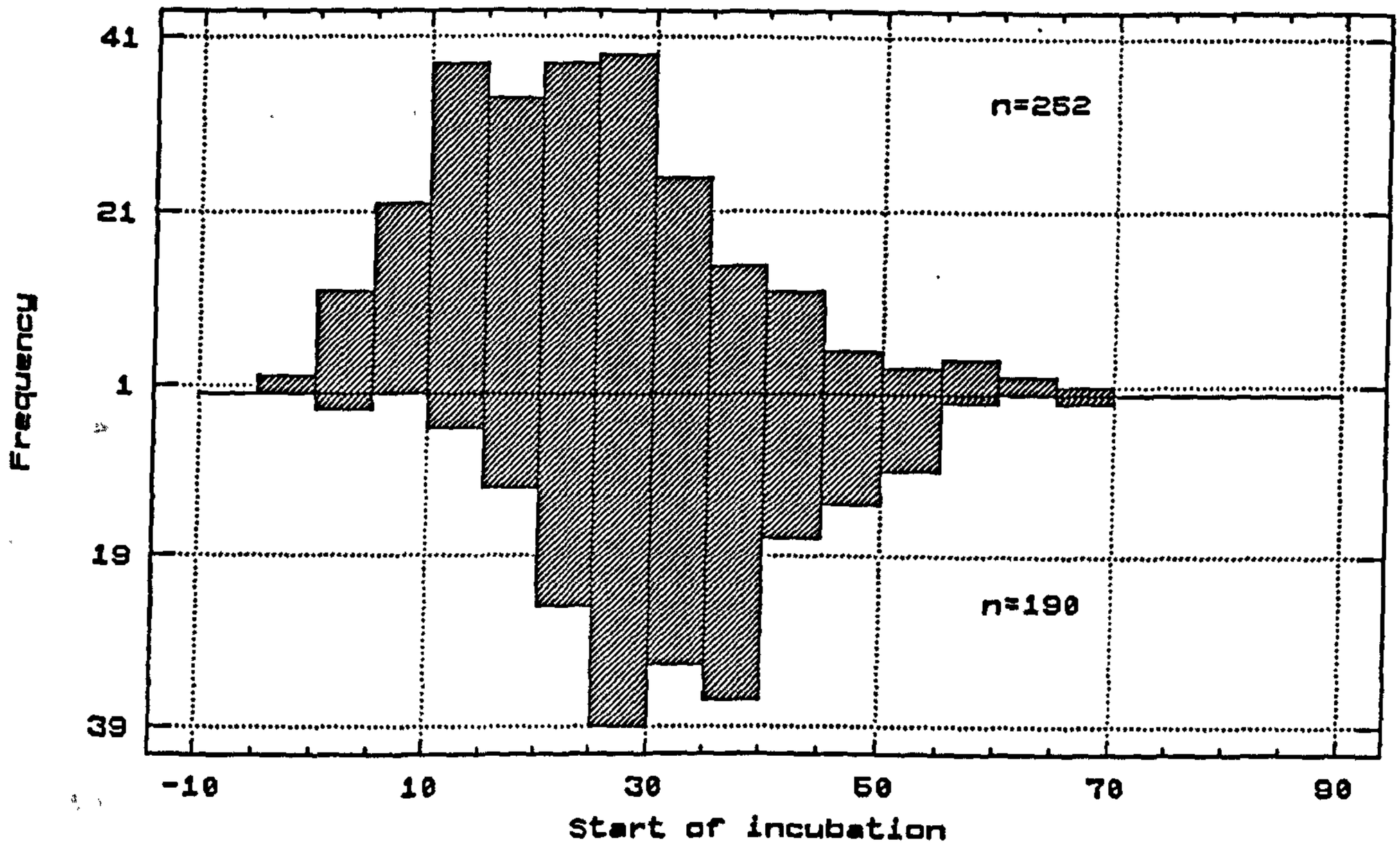


Figure 5.5 Start of incubation in tawny owls in five-day classes in Kielder (upper) and Glenbranter (lower) during 1984-90.

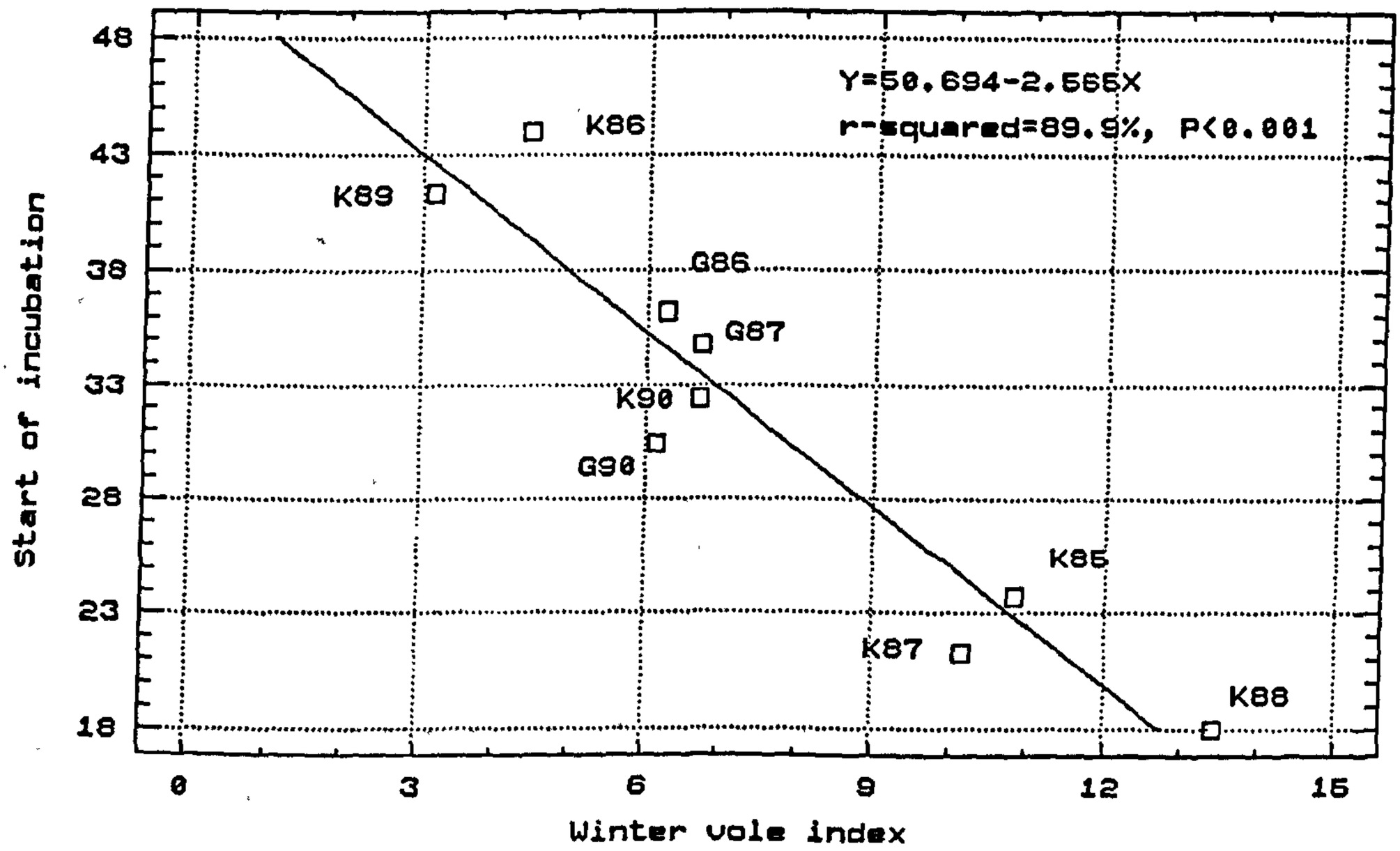


Figure 5.6 Relationship between the mean start of incubation in tawny owls and the mean winter vole index. Each point relates to a study/area year, K = Kielder and G = Glenbranter.

P<0.001). In Kielder the range in individual SIC spanned 74 days during 1980-1990 and in Glenbranter 74 days during 1984-90 (Table 5.6). Variation in the mean annual SIC showed a 28 d difference from 16 March (1984) to 13 April (1986) in Kielder (mean 24 March) and an 18 d difference from 22 March (1984) to 9 April (1989) in Glenbranter (mean 2 April).

5.3.2.2 The relationship between food supply and the start of incubation

To investigate the relationship between vole abundance and the start of incubation, the mean autumn vole index from the previous year and mean spring index from the current year were plotted against the mean SIC for each year that vole indices were available from both study areas (1985-1990). There were significant negative relationships between the SIC and both the spring vole index (r=-0.845, df=11, P<0.001) and the autumn vole index (r=-0.795, df=8, P<0.05). However, an even better relationship was obtained with the winter vole index (autumn index+spring index/2). This relationship explained 89.9% of the annual variation in the mean SIC (Figure 5.6) and suggested that vole abundance in the winter had a greater effect on the start of breeding than either vole abundance in autumn or spring. Only three data points from Glenbranter could be used in this regression as vole abundance was not measured in the remaining autumns (Figure 5.6). Excluding these points from Glenbranter had little effect on the model (Kielder only Y=50.271-2.424X, n=7, r-squared=92.5%, P<0.001).

5.3.2.3 Weather and the start of incubation

As much of the variability in the SIC was related to winter vole abundance (Figure 5.6), it was unlikely that any other single variable would show a significant relationship with SIC. To investigate the possible effects of weather a similar procedure was employed as in section 5.3.1. There were no significant relationships in either autumn or winter when SIC was plotted individually against the five weather variables (Table 5.4). Taken

together with the previous section, these analyses strongly suggest that winter vole abundance had the major impact on SIC and that, over the conditions experienced in my study, weather had little influence.

5.3.3 Clutch size and losses during incubation

Throughout this section unless otherwise stated, clutch size is calculated from pairs laying at least one egg, with clutches deserted through observer disturbance removed (section 5.2.5).

5.3.3.1 Variation in clutch size between study areas and years

In Kielder clutches ranged from one to six eggs (Table 5.7). The modal clutch size was three eggs with four and two egg clutches the next most frequent. Clutches of five eggs were uncommon and there were only two one-egg clutches and one clutch of six. The clutch size distribution was different in Glenbranter, with clutches of two and three eggs equally abundant, clutches of four rare and clutches of five or six unrecorded. Mean clutch size was 0.64 of an egg larger in Kielder than Glenbranter (1984-90, Mann-Whitney U-test, $Z=-8.03$, $P<0.001$) (Table 5.8).

There were significant variations in clutch size between years both in Kielder (1980-90, Kruskal-Wallis, test statistic = 97.10, $P<0.001$; 1984-90, test statistic = 58.20, $P<0.001$) and to a lesser but still significant extent in Glenbranter (1984-90, test statistic = 27.73, $P<0.001$). In Kielder, the largest mean annual clutch size was 3.63 eggs (1987) and the smallest was 2.07 (1989), whereas in Glenbranter the equivalent figures were 2.90 (1984) and 2.17 (1989) (Table 5.8).

5.3.3.2 The relationship between food supply and clutch size

More of the variation in clutch size (88.6%) was explained by the spring vole index (Figure 5.7) than by winter (73.8%) or previous autumn (33.8%) vole indices. The relationship between clutch size and the spring vole index was similar in both study areas (Kielder

Table 5.7 Annual clutch sizes of tawny owls in Kielder and Glenbranter.

Year	Clutch size (%)						Total clutches
	1	2	3	4	5	6	
Kielder							
80	0	6(33.3)	12(66.7)	0	0	0	18
81	0	9(22.0)	16(39.0)	16(39.0)	0	0	41
82	1(2.9)	18(52.9)	12(35.3)	3 (8.8)	0	0	34
83	0	9(90.0)	1(10.0)	0	0	0	10
84	1(2.3)	6(14.0)	13(30.2)	19(44.2)	4 (9.3)	0	43
85	0	12(27.3)	23(52.3)	9(20.5)	0	0	44
86	0	2(50.0)	2(50.0)	0	0	0	4
87	0	3 (6.3)	17(35.4)	23(47.9)	5(10.4)	0	48
88	0	5(10.0)	23(46.0)	19(38.0)	2 (4.0)	1(2.0)	50
89	0	13(92.9)	1 (7.1)	0	0	0	14
90	0	15(29.4)	26(51.0)	10(17.6)	0	0	51
80-90	2(0.6)	98(27.5)	146(40.9)	99(27.7)	11 (3.1)	1(0.3)	357
84-90	1(0.4)	56(22.0)	105(41.3)	80(31.5)	11 (4.3)	1(0.4)	254
Glenbranter							
84	0	5(25.0)	12(60.0)	3(15.0)	0	0	20
85	0	11(55.0)	9(45.0)	0	0	0	20
86	0	7(43.8)	9(56.3)	0	0	0	16
87	1(3.4)	12(41.4)	15(51.7)	1 (3.4)	0	0	29
88	0	20(64.5)	11(35.5)	0	0	0	31
89	2(6.7)	21(70.0)	7(23.3)	0	0	0	30
90	0	14(31.1)	26(57.8)	5(11.1)	0	0	45
84-90	3(1.6)	90(47.1)	89(46.6)	9 (4.7)	0	0	191

Table 5.8 Mean annual clutch size and mean egg loss per clutch in tawny owls laying at least one egg in Kielder and Glenbranter. In some years the sample size between clutch size and egg loss differs because clutches which were deserted due to observer disturbance have been excluded from the egg loss calculations.

Year	Clutch (mean)	n	SE	SD	Range	Mode	Median	SS	SK	Egg loss(n)
Kielder										
80	2.67	18	0.11	0.48	2-3	3	3.0	-1.34	-1.38	0.53(15)
81	3.17	41	0.12	0.77	2-4	4	3.0	-0.81	-1.61	0.29(38)
82	2.50	34	0.12	0.71	1-4	2	2.0	1.30	-0.09	0.21(33)
83	2.10	10	0.10	0.32	2-3	2	2.0	4.08	6.45	0.56(9)
84	3.44	43	0.14	0.93	1-5	4	4.0	-1.25	-0.09	0.24(42)
85	2.93	44	0.10	0.70	2-4	3	3.0	0.25	-1.15	0.16(43)
86	2.50	4	0.29	0.58	2-3	3	2.5	0.00	-2.45	0.25(4)
87	3.63	48	0.11	0.76	2-5	4	4.0	-0.40	-0.27	0.21(48)
88	3.42	50	0.11	0.81	2-6	3	3.0	1.47	1.56	0.13(48)
89	2.07	14	0.07	0.27	2-3	2	2.0	5.72	10.70	0.14(14)
90	2.90	51	0.10	0.70	2-4	3	3.0	0.40	-1.31	0.20(51)
80-90	3.06	357	0.04	0.85	1-6	3	3.0	1.87	-1.76	0.22(345)
84-90	3.19	254	0.05	0.85	1-6	3	3.0	1.13	-1.17	0.18(250)
Glenbranter										
84	2.90	20	0.14	0.64	2-4	3	3.0	0.08	-0.23	0.30(20)
85	2.45	20	0.11	0.51	2-3	2	2.0	0.39	-1.99	0.07(16)
86	2.56	16	0.13	0.51	2-3	3	3.0	-0.46	-1.81	0.13(16)
87	2.55	29	0.12	0.63	1-4	3	3.0	-0.46	-0.04	0.07(29)
88	2.35	31	0.09	0.49	2-3	2	2.0	1.45	-1.94	0.14(29)
89	2.17	30	0.10	0.53	1-3	2	2.0	0.43	0.51	0.41(27)
90	2.80	45	0.09	0.63	2-4	3	3.0	0.45	-0.64	0.35(43)
84-90	2.55	191	0.04	0.61	1-4	2	3.0	1.38	-1.08	0.23(180)

Egg loss (n) = the mean number of eggs that failed to hatch per clutch (number of clutches)

SS = Standardized Skewness coefficient; SK = Standardized Kurtosis coefficient (see Table 5.4 for further details of these two coefficients).

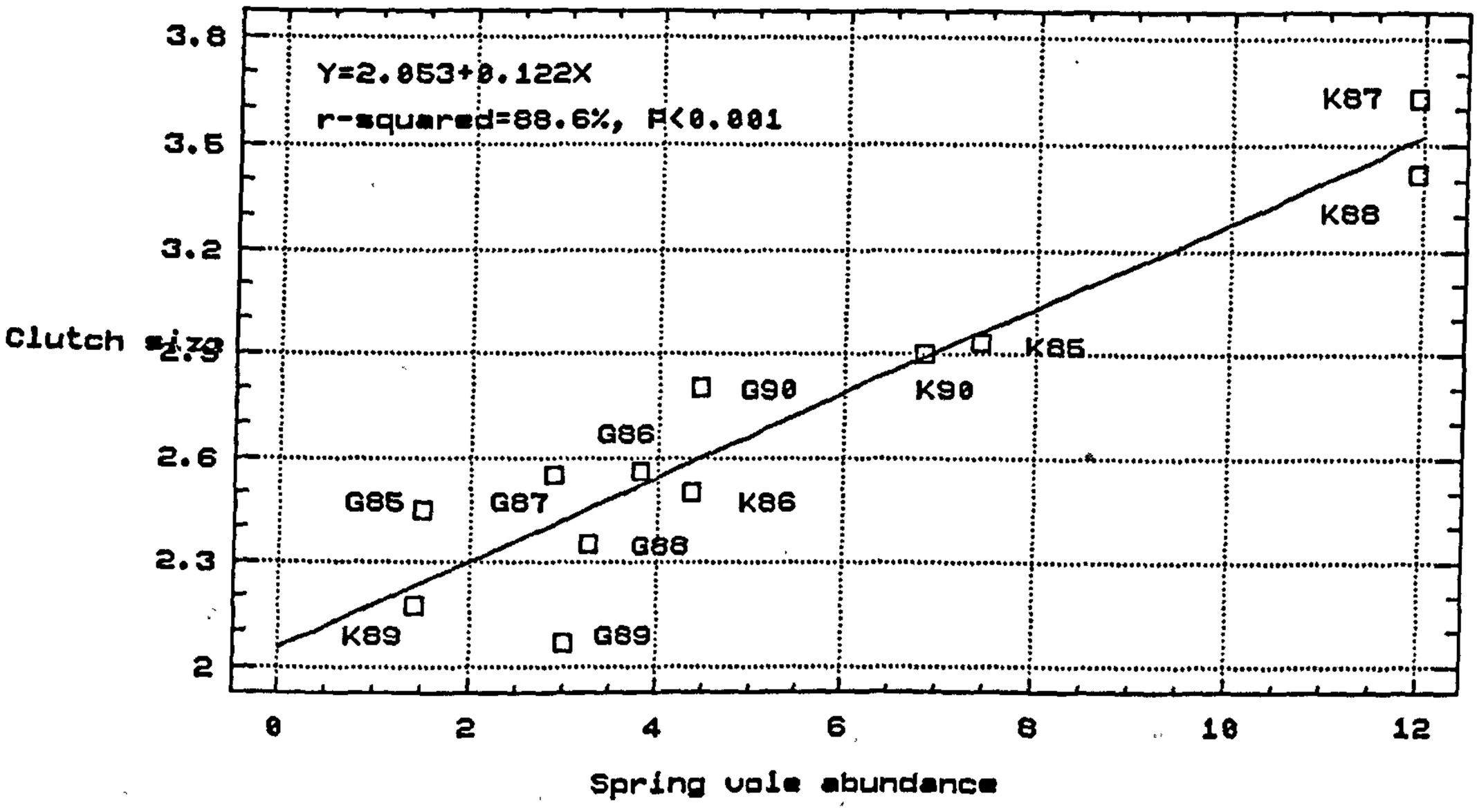


Figure 5.7 Relationship between mean clutch size in tawny owls and the mean spring vole index. Each point relates to a study/area year, K = Kielder and G = Glenbranter

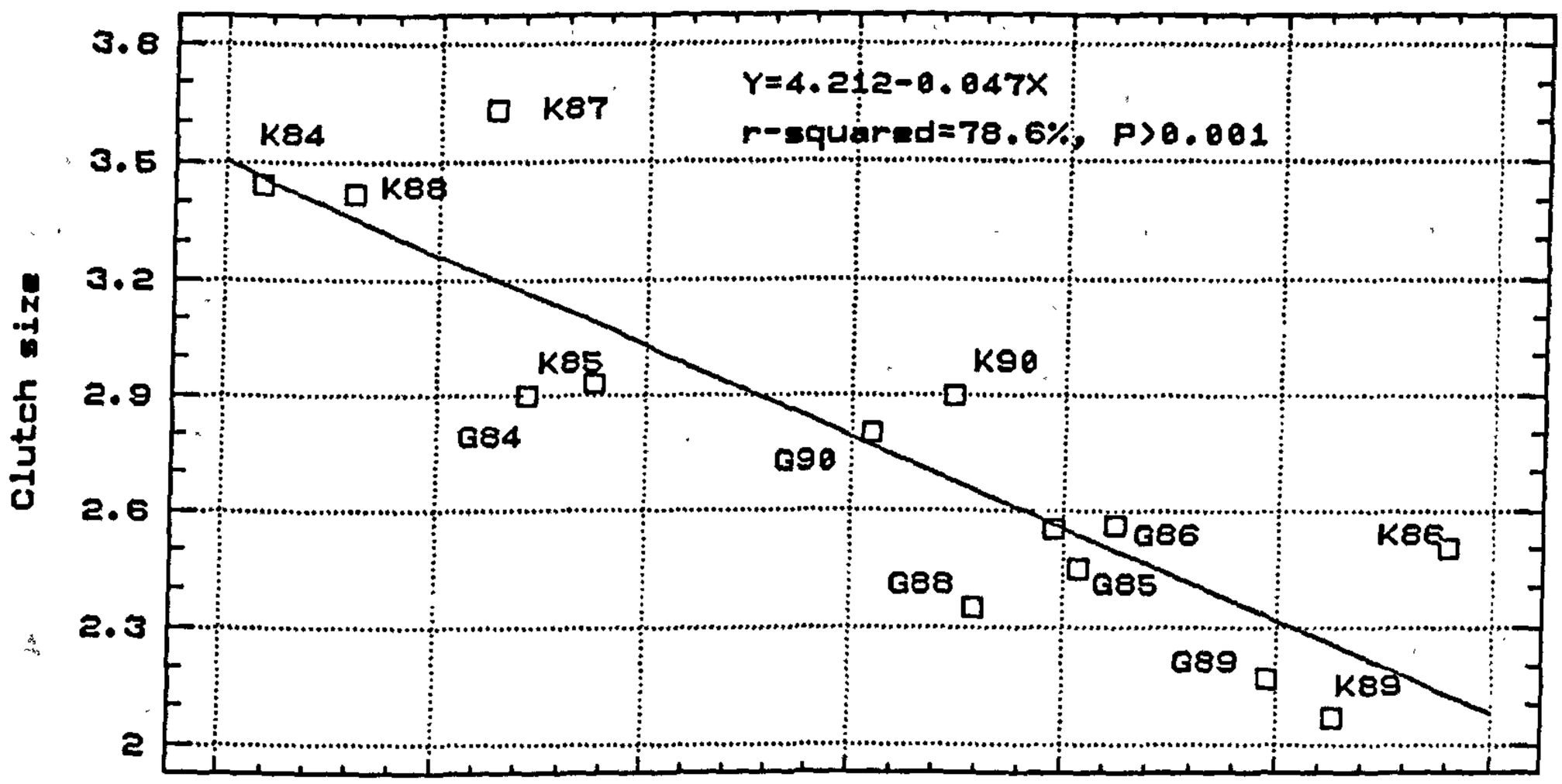


Figure 5.8 Relationship between mean clutch size and the mean start of incubation in tawny owls during 1984-90. Each point relates to a study/area year, K = Kielder and G = Glenbranter

Y=1.764+0.151X, n=6, r-squared=96.0%, P<0.001; Glenbranter Y=2.087+0.136X, n=6, r-squared=60.8%, P=0.07) but with more scatter around the regression model for Glenbranter.

The start of incubation (SIC) during the same period was also significantly related to clutch size, explaining 78.6% in the variation of clutch size (Figure 5.8). However, in a step-wise multiple regression analysis using both spring vole abundance, SIC and female weight as independent variables; spring vole abundance was selected as the most highly correlated variable with clutch size. Using spring vole abundance only in the model accounted for 87% of the variability in clutch size, adding in female weight (taken during the nestling period) increased this to 92% while SIC did not significantly add to the explanatory power of the model (Table 5.9). SIC was less important, largely because it was independently related to vole abundance (section 5.3.2.2).

5.3.3.3 Clutch size in relation to the start of incubation

A seasonal decline in clutch size occurred in both study areas and in most years (Table 5.10). There were also pronounced annual variations in the SIC for clutches of a similar size. The mean annual SIC for clutches of two, three and four eggs varied by 24.6, 28.5 and 11.7 days respectively over 11 years in Kielder and by 19.3, 11.4 and 12.3 days respectively over seven years in Glenbranter (Table 5.10).

Although there was much between-year variation in SIC for clutches of the same size, there was an overall seasonal decline in clutch size which was similar in both study areas, but with clutches of three and four being laid earlier in Kielder (Figure 5.9).

5.3.3.4 Weather and clutch size

Weather was not expected to have a great influence on clutch size because much of the variation (88.6%) had already been explained by spring vole abundance. A similar analysis was undertaken to that in

Table 5.9 A multiple regression model using two variables explained 92% of the variation in mean annual clutch size of tawny owls (F=64.77, df=2,9, P<0.001). This model uses data from Kielder and Glenbranter (1985-1990).

Independent variable	Coefficient	SE	t	Significance level
Constant	-1.087	1.202	-0.905	0.389
Spring vole abundance	0.093	0.016	5.851	0.000
Female body weight	0.006	0.002	2.617	0.028

Table 5.10 Start of incubation (SIC) for each clutch size of tawny owls by year in Kielder and Glenbranter.

Year	Clutch size (n)					
	1	2	3	4	5	6
Kielder						
80	-	52.7(6)	36.8(11)	-	-	-
81	-	40.7(9)	25.8(16)	16.4(16)	-	-
82	34.0(1)	29.8(18)	24.7(12)	14.3(3)	-	-
83	-	40.7(9)	44.0(1)	-	-	-
84	-	29.5(6)	15.5(13)	12.4(19)	13.5(4)	
85	-	34.5(12)	22.8(23)	11.9(9)	-	-
86	-	51.0(2)	37.0(2)	-	-	-
87	-	53.0(2)	23.6(17)	16.7(23)	21.8(5)	-
88	-	28.4(5)	20.5(23)	14.2(19)	6.0(2)	6.0(1)
89	-	42.8(13)	22.0(1)	-	-	-
90	-	42.6(15)	29.9(26)	23.6(10)	-	-
80-90	34.0(1)	38.4(97)	25.0(145)	15.5(99)	15.7(11)	6.0(1)
84-90	-	38.8(55)	23.5(105)	15.4(80)	15.7(11)	6.0(1)
Glenbranter						
84	-	23.8 (5)	23.9(12)	12.3 (3)	-	-
85	-	38.6(11)	31.3 (9)	-	-	-
86	-	43.1 (7)	30.8 (9)	-	-	-
87	51.0(1)	39.8(12)	30.2(15)	17.0 (1)	-	-
88	-	35.8(20)	27.2(10)	-	-	-
89	33.0(2)	42.1(20)	35.3 (7)	-	-	-
90	-	36.7(14)	28.2(26)	24.6 (5)	-	-
84-90	39.0(3)	38.1(89)	29.0(88)	19.7 (9)	-	-

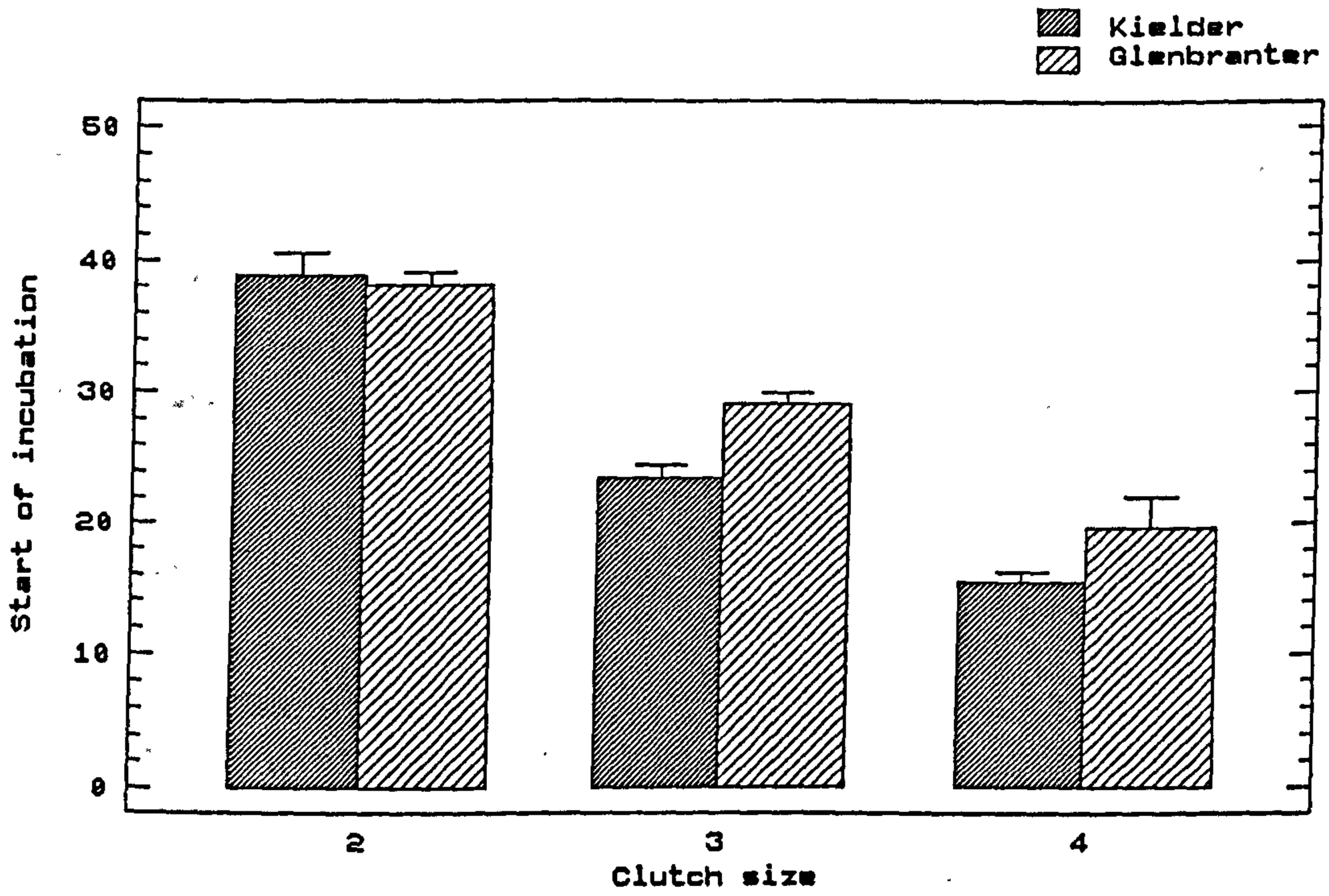


Figure 5.9 The relationship between the mean start of incubation (SIC) and clutch size (with SE bars) in tawny owls during 1984-90 in Kielder and Glenbranter. There was no significant difference in SIC between study areas for clutches of two (Mann-Whitney U-test Z=-0.13, NS) and four (Z=1.18, NS) but there was for clutches of three eggs (Z=4.13, P<0.001). Clutches of one, five and six have been excluded because there were so few.

Table 5.11 The incidence of egg mortality in three categories in relation to eggs that hatched by clutch size (Kielder and Glenbranter (1984-90).

Clutch size	Kielder n(%)					Glenbranter n(%)			
	cracked	unhatched*	deserted	hatched	total	unhatched*	deserted	hatched	total
1	0 (0.0)	0 (0.0)	1(100.0)	0 (0.0)	1(100)	0 (0.0)	1(50.0)	1(50.0)	2(100)
2	1 (1.0)	4 (3.8)	8 (7.7)	91(87.5)	104(100)	5 (3.1)	12 (7.3)	147(89.6)	164(100)
3	0 (0.0)	11 (3.5)	0 (0.0)	304(96.5)	315(100)	13 (5.0)	9 (3.4)	239(91.6)	261(100)
4	1 (0.3)	13 (4.0)	4 (1.3)	302(94.4)	320(100)	1 (2.8)	0 (0.0)	35(97.2)	36(100)
5	0 (0.0)	2 (3.6)	0 (0.0)	53(96.4)	55(100)	-	-	-	-
6	0 (0.0)	1(16.7)	0 (0.0)	5(83.3)	6(100)	-	-	-	-
Overall	2	31	13	755	801	19	22	422	463
% of total	0.2	3.9	1.6	94.3	100.0	4.1	4.8	91.1	100

* eggs that were fully incubated but failed to hatch

section 5.3.1 (Table 5.4). There were no significant relationships between clutch size and the five weather variables in autumn, and only one in spring (Table 5.4). The significant relationship in spring was with the number of days with air frost. However, it was a relatively weak relationship (r=0.49, n=17, P=0.04) which did not persist when correlation coefficients were calculated separately for each study area (Kielder r=0.49, n=9, NS; Glenbranter r=0.17, n=7, NS). This analysis suggested that weather had little effect on clutch size.

5.3.3.5 Egg mortality

Eggs that failed to hatch were placed into three categories.

A. Cracked eggs (all Kielder) which then lost weight quickly and did not hatch. None were noticeably thin-shelled.

B. Fully incubated eggs that failed to hatch.

C. Eggs that failed to hatch due to natural desertion of the clutch.

In total, egg failures during 1984-90 amounted to 0.18 egg per clutch in Kielder and 0.23 egg per clutch in Glenbranter (Table 5.8), with no significant differences between study areas (Mann-Whitney U-test, Z=0.486, NS) or between years in either Kielder (Kruskal-Wallis one-way analysis by ranks, test statistic = 2.11, NS) or Glenbranter (test statistic = 9.75, NS).

Of 801 eggs laid in Kielder during 1984-90 only 5.7% failed to hatch compared to 8.9% of 463 laid in Glenbranter during the same period (Table 5.11). These egg failure rates were significantly different between study areas (chi-squared with Yates correction = 3.96, df=1, P<0.05), resulting from proportionally more eggs being deserted in Glenbranter (with deserted eggs removed from the total eggs failing, chi-squared with Yates correction = 0.00, df=1, NS). The incidence of unhatched (fully incubated) eggs showed no significant relationship with clutch size and was at a similar level in both study areas (Table 5.11), but proportionally more

desertions occurred in clutches of 1-2 eggs than in clutches of 3-4 eggs in both Glenbranter (chi-squared with Yates correction = 4.23, df=1, P<0.05) and Kielder (chi-squared with Yates correction = 28.8, df=1, P<0.001).

These results show that relatively few eggs failed to hatch, and suggest that the incidence of unhatched fully-incubated eggs occurred at random among clutches, while nest desertions were more prevalent in the smaller clutches, particularly in Glenbranter.

5.3.3.6 Repeat clutches

Pairs deserted nests due to observer disturbance (Table 5.1) and natural causes; both are amalgamated in this section to investigate the incidence of relaying.

The proportion of pairs deserting nests was significantly higher in Glenbranter (35.1%) than Kielder (20.7%) (Table 5.12), but significantly fewer of these pairs relaid in Glenbranter (17.9%) than Kielder (40.5%). Significant differences emerged between study areas in the stage when failures occurred, whether during the laying, incubation or nestling stages (chi-squared = 8.45, df=2, P<0.05) (Table 5.13). In Glenbranter there were fewer desertions during laying but far more during the nestling stage than in Kielder. The proportion of pairs failing during incubation was similar in both areas. Combining study areas, of pairs failing during egg-laying 79.2% relaid, compared with 33.9% during incubation and only 3.6% during the nestling stage (chi-squared = 23.40, df=2, P=<0.001).

There was no significant relationship between the proportion of pairs deserting and spring vole abundance (r=-0.267, df=12, NS) with study areas combined because desertions largely resulted from observer disturbance. However, there was a significant relationship between the proportion of pairs relaying after desertion and spring vole abundance (r=0.708, df=12, P<0.01).

Table 5.12 Proportion of tawny owl pairs deserting and relaying in Kielder (1980-1990) and Glenbranter (1984-1990).

	Kielder	Glenbranter
(a) No. pairs laying	357	191
(b) No. pairs deserting (% of a)	74 (20.7)	67 (35.1)
(c) No. of pairs relaying (% of b)	30 (40.5)	12 (17.9)

The proportion of pairs deserting vs not deserting was significantly higher in Glenbranter than Kielder (chi-squared with Yates correction = 7.14, df=1, P<0.001).

The proportion of pairs relaying vs not relaying was significantly higher in Kielder compared to Glenbranter (chi-squared with Yates correction = 7.56, df=1, P<0.01).

Table 5.13 The stage when tawny owl nests were deserted in relation to the proportion of pairs relaying in Kielder (1980-1990) and Glenbranter (1984-1990). A = deserted during egg laying, B = during incubation, C = during the nestling stage.

	Kielder			Glenbranter			Overall		
	A	B	C	A	B	C	A	B	C
No. pairs deserting	18	34	22	6	28	33	24	62	55
% of A+B+C	24.3	46.0	29.7	9.0	41.8	49.2	17.0	44.0	39.0
No. pairs relaying	14	14	2	5	7	0	19	21	2
% pairs relaying	77.7	41.2	9.1	83.3	25.0	0.0	79.2	33.9	3.6

In 45 repeat clutches it was possible to measure the interval between the desertion of one clutch and the start of incubation of the next. As most repeat clutches resulted from observer disturbance, the exact day of desertion was usually known. The relaying interval increased significantly the further a pair progressed with the initial attempt (Figure 5.10). The regression coefficients were similar in both study areas (Kielder b=1.43, Glenbranter b=1.54) justifying pooling the data. Most pairs that deserted during laying started to incubate their next clutch within 10 days. At the other extreme, the relaying interval exceeded 40 days for the few pairs which relaid after deserting small chicks. No repeat clutches were recorded from pairs which failed with chicks over 6 days old.

As expected, clutches deserted during egg-laying were significantly smaller in both study areas than clutches deserted after completion (Table 5.14). Whether a clutch was deserted during laying or incubation did not seem to influence the size of the replacement clutch or the brood produced from it. However, there were significant differences between areas in both replacement clutch and brood size, both being larger in Kielder.

As a result of repeat clutches, some females produced considerably more eggs in one year than the maximum clutch size of 6 eggs recorded during the study. The most eggs laid by individual females occurred in 1991 in Kielder. One female laid 3 eggs then deserted and laid 6 eggs at another site, from which five chicks were reared. Another female laid complete clutches of 3, 4 and 3 eggs in the same nestbox. The first and second clutches were deserted after visits to the nest. She failed in the end because the 10 eggs in the box could not be properly incubated. This female had only one nestbox in her territory, and was therefore unable to move to a new nest site to relay as most females did.

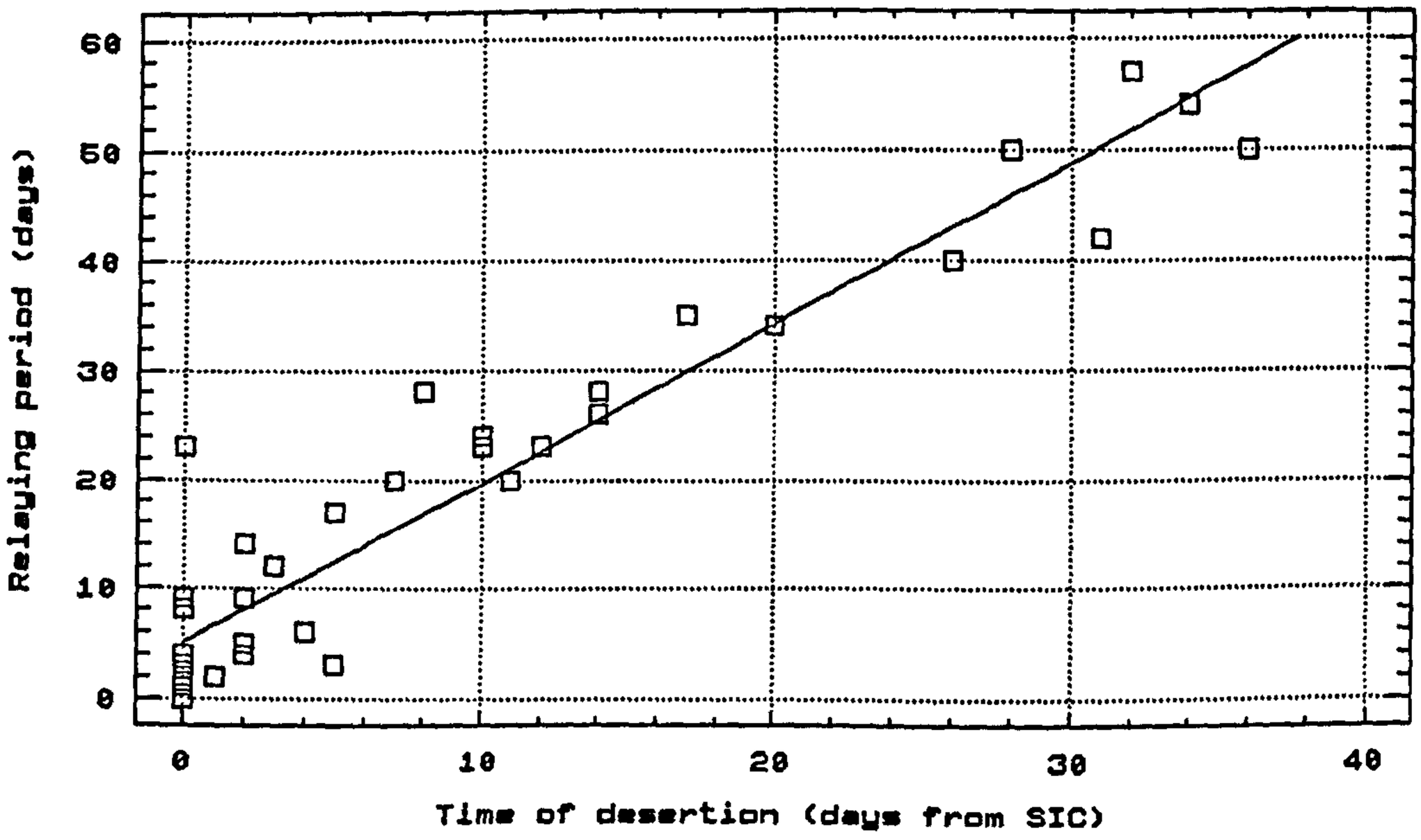


Figure 5.10 Relaying period (days from desertion of one clutch to the start of incubation of the next) in relation to when the first clutch was deserted (days from the start of incubation) (Y=5.104+1.455X, n=45, P<0.001, r-squared=90.13%). Data from Glenbranter and Kielder combined.

Table 5.14 Mean (n) SE of initial and repeat clutches and brood sizes from repeat clutches of tawny owls in Kielder (1980-1990) and Glenbranter (1984-1990).

Study area and time of desertion	Initial clutch clutch size (A)	Repeat clutch size (B)	Brood size of repeat clutch (C)
Kielder			
(1) Deserted during laying	1.28 (18) 0.16	3.22 (18) 0.26	2.50 (18) 0.35
(2) Deserted after incubation commenced	3.39 (18) 0.14	3.11 (18) 0.20	2.00 (18) 0.31
Glenbranter			
(3) Deserted during laying	1.20 (5) 0.20	2.40 (5) 0.40	1.40 (5) 0.40
(4) Deserted after incubation commenced	3.00 (7) 0.22	2.29 (7) 0.42	1.14 (7) 0.59

Mann Whitney U-Tests

	A	B	C
1 v 2	***	NS	NS
1 v 3	NS)		
2 v 4	NS }	*	*
3 v 4	*	NS	NS

	A v B
1	*
2	NS
3	NS
4	NS

5.3.4 Brood size and losses during the nestling period

Throughout this section brood size refers to the number of chicks raised to fledging by pairs which laid at least one egg, and included pairs which failed to rear any chicks. Successful brood size is sometimes used and this refers to pairs that reared at least one chick to fledging. Fledging was used to denote when a nestling left the nest site. The smaller sample sizes for brood sizes compared to clutch sizes resulted from the exclusion of clutches which were deserted (5.2.5).

5.3.4.1 Variation in brood size between study areas and years

In Kielder during 1980-90 brood sizes ranged from zero to five (Table 5.15). The modal brood was two chicks (1980-1990) but broods of three chicks were almost as frequent. Broods of four chicks were more frequent than broods of two. Twenty-eight (8.2%) clutches failed to produce any chicks but at the other extreme five chicks were reared on five occasions.

The modal brood size during 1984-90 was the same in Glenbranter, but like clutch size, the shape of the brood size distribution was different from Kielder (Table 5.15). The most frequent brood was two chicks but broods of zero and one were similarly abundant, whereas broods of four chicks were rare. Thirty-nine clutches (22.2%) failed to rear chicks, a higher proportion than in Kielder.

During 1984-90, tawny owls in Kielder reared on average 2.54 chicks per clutch (n=246). This was significantly larger (by 1.04 chicks) than the mean brood size of 1.50 (n=176) in Glenbranter (Mann-Whitney U-test, $Z=-0.8.65$, $P<0.001$) (Table 5.16). Mean brood size also differed significantly between years, both in Kielder (Kruskal-Wallis, test statistic = 65.07, $P<0.001$) and Glenbranter (test statistic = 26.93, $P<0.001$). This difference still persisted when broods of zero were excluded (Kielder, test statistic = 73.03, $P<0.001$ and Glenbranter test statistic = 15.28, $P<0.05$). The

Table 5.15 Annual brood sizes of tawny owl in Kielder and Glenbranter.

Year	Brood size (%)						
	0	1	2	3	4	5	Total broods
Kielder							
80	2(13.3)	2(13.3)	5(33.3)	6(40.0)	0	0	15
81	6(15.8)	2 (5.3)	10(26.3)	16(42.1)	4(10.5)	0	38
82	2 (6.1)	9(27.3)	18(54.5)	4(12.1)	0	0	33
83	1(11.1)	5(55.6)	3(33.3)	0	0	0	9
84	2 (4.8)	0	7(16.7)	16(38.1)	15(35.7)	2(4.8)	42
85	4 (9.3)	6(14.0)	17(39.5)	13(30.2)	3 (7.0)	0	43
86	0	1(25.0)	3(75.0)	0	0	0	4
87	3 (6.3)	1 (2.1)	4 (8.3)	17(35.4)	20(41.7)	3(6.3)	48
88	4 (9.1)	7(15.9)	18(40.9)	11(25.0)	4 (9.1)	0	44
89	2(14.3)	6(42.9)	6(42.9)	0	0	0	14
90	2 (3.9)	4 (7.8)	16(31.4)	21(41.2)	8(15.7)	0	51
80-90	28 (8.2)	43(12.6)	107(31.4)	104(30.5)	54(15.8)	5(1.5)	341
84-90	17 (6.9)	25(10.2)	71(28.9)	78(31.7)	50(20.3)	5(2.0)	246
Glenbranter							
84	4(20.0)	4(20.0)	6(30.0)	6(30.0)	0	0	20
85	1 (6.7)	3(20.0)	11(73.3)	0	0	0	15
86	3(18.8)	3(18.8)	8(50.0)	2(12.5)	0	0	16
87	2 (7.1)	5(17.9)	12(42.9)	8(28.6)	1 (3.6)	0	28
88	9(32.1)	9(32.1)	8(28.6)	2 (7.1)	0	0	28
89	12(46.2)	8(30.8)	6(23.1)	0	0	0	26
90	8(18.6)	9(20.9)	15(34.9)	11(25.6)	0	0	43
84-90	39(22.2)	41(23.3)	66(37.5)	29(16.5)	1 (0.6)	0	176

Table 5.16 Mean annual brood sizes (chicks fledging) of tawny owl pairs laying at least one egg in Kielder and Glenbranter with the effects of observer disturbance removed. Brood sizes at hatching and fledging at successful nests are also included.

Year	Brood size	n	SE	SD	Range	Mode	Median	SS	SK	Chick loss (n)	Brood size at hatching (n)	Successful brood size(n)
Kielder												
80	2.00	15	0.28	1.07	0-3	3	2.0	-1.28	-0.32	0.20(15)	2.36(14)	2.31(13)
81	2.26	38	0.20	1.22	0-4	3	3.0	-1.82	-0.46	0.63(38)	3.06(36)	2.69(32)
82	1.73	33	0.13	0.76	0-3	2	2.0	-0.91	0.20	0.52(33)	2.31(32)	1.84(31)
83	1.22	9	0.22	0.67	0-2	1	1.0	-0.31	-0.02	0.33(9)	1.75(8)	1.38(80)
84	3.14	42	0.17	1.07	0-5	3	3.0	-2.77	2.48	0.10(42)	3.40(40)	3.30(40)
85	2.12	43	0.16	1.05	0-4	2	2.0	-0.99	-0.25	0.67(43)	2.86(42)	2.33(39)
86	1.75	4	0.25	0.50	1-2	2	2.0	-1.63	1.63	0.50(4)	2.25(4)	1.75(4)
87	3.23	48	0.17	1.17	0-5	4	3.0	-3.67	2.68	0.19(48)	3.56(46)	3.44(45)
88	2.09	44	0.16	1.07	0-4	2	2.0	-0.51	-0.37	1.34(44)	3.35(48)	2.30(40)
89	1.29	14	0.19	0.73	0-2	2	1.0	-0.79	-0.56	0.64(14)	1.93(14)	1.50(12)
90	2.57	51	0.14	0.98	0-4	3	3.0	-1.73	0.49	0.14(51)	2.82(49)	2.67(49)
80-90	2.38	341	0.06	1.18	0-5	2	2.0	-1.98	-1.59	0.49(341)	2.96(333)	2.59(313)
84-90	2.54	246	0.08	1.18	0-5	3	3.0	-2.36	-1.04	0.48(246)	3.11(243)	2.73(229)
Glenbranter												
84	1.70	20	0.25	1.13	0-3	3	2.0	-0.57	-1.14	0.90(20)	2.89(18)	2.13(16)
85	1.67	15	0.16	0.62	0-2	2	2.0	-2.83	2.07	0.80(15)	2.44(16)	1.79(14)
86	1.56	16	0.24	0.96	0-3	2	2.0	-0.75	-0.48	0.88(16)	2.44(16)	1.92(13)
87	2.04	28	0.18	0.96	0-4	2	2.0	-0.74	-0.02	0.46(28)	2.48(29)	2.19(26)
88	1.11	28	0.18	0.96	0-3	1	1.0	0.69	-0.99	1.11(28)	2.32(28)	1.63(19)
89	0.77	26	0.16	0.82	0-2	0	1.0	0.97	-1.38	1.00(26)	2.09(23)	1.43(14)
90	1.67	43	0.16	1.06	0-3	2	2.0	-0.79	-1.47	0.81(43)	2.68(40)	2.06(35)
84-90	1.50	176	0.08	1.03	0-4	2	2.0	-0.43	-2.74	0.85(176)	2.48(170	1.93(137))

Chick loss (n) = the mean number of nestlings dying per pair laying (number of clutches).

Brood size at hatching = mean brood size from nests where at least one chick hatched.

Successful brood size = mean number of chicks fledging from nests where at least one chick was reared.

SS = Standardized Skewness coefficient; SK = Standardized Kurtosis coefficient (see Table 5.4 for further details of these two coefficients)

largest mean annual brood size in Kielder was 3.23 in 1987 and the smallest was 1.22 in 1983, whereas in Glenbranter brood sizes ranged from 2.04 in 1987 to 0.77 in 1989.

5.3.4.2 The relationship between food supply and brood size

To investigate relationships between vole abundance and the number of chicks reared, the mean spring and summer vole indices were plotted against mean brood size by study area for each year that vole abundance was measured (1984-1990). The summer vole index explained 58.4% of the variation in brood size and 56.2% in successful brood size, whereas corresponding values using the spring vole index were 60.2% and 65.1%. However, a vole index mid-way between those for the spring and summer (spring index+summer index/2) explained 92.1% (Figure 5.11) and 95.7% respectively of the variance in brood and successful brood sizes.

5.3.4.3 Brood size and weather

As much of the variability in brood size was related to spring/summer vole abundance (Figure 5.11), it was unlikely that any other factor would have a major influence. Brood size was most likely to be influenced by adverse weather conditions during the hatching and nestling period; resulting from reduced prey deliveries to the nest. To investigate this aspect, brood size was used as the dependent variable in a regression analysis with mean daily temperature, total rainfall and the number of days with 10 mm or more of rain (section 5.2.7) during the period April-June as independent variables. There were no significant relationships.

5.3.4.4 Nestling mortality

During 1984-90, mean nestling mortality in Glenbranter, at 0.85 chicks per pair laying (n=176) was significantly higher than the 0.48 chicks per pair (n=246) in Kielder during 1984-90 (Mann-Whitney U-test, $Z=4.52$, $P<0.001$) (Table 5.16). There was also

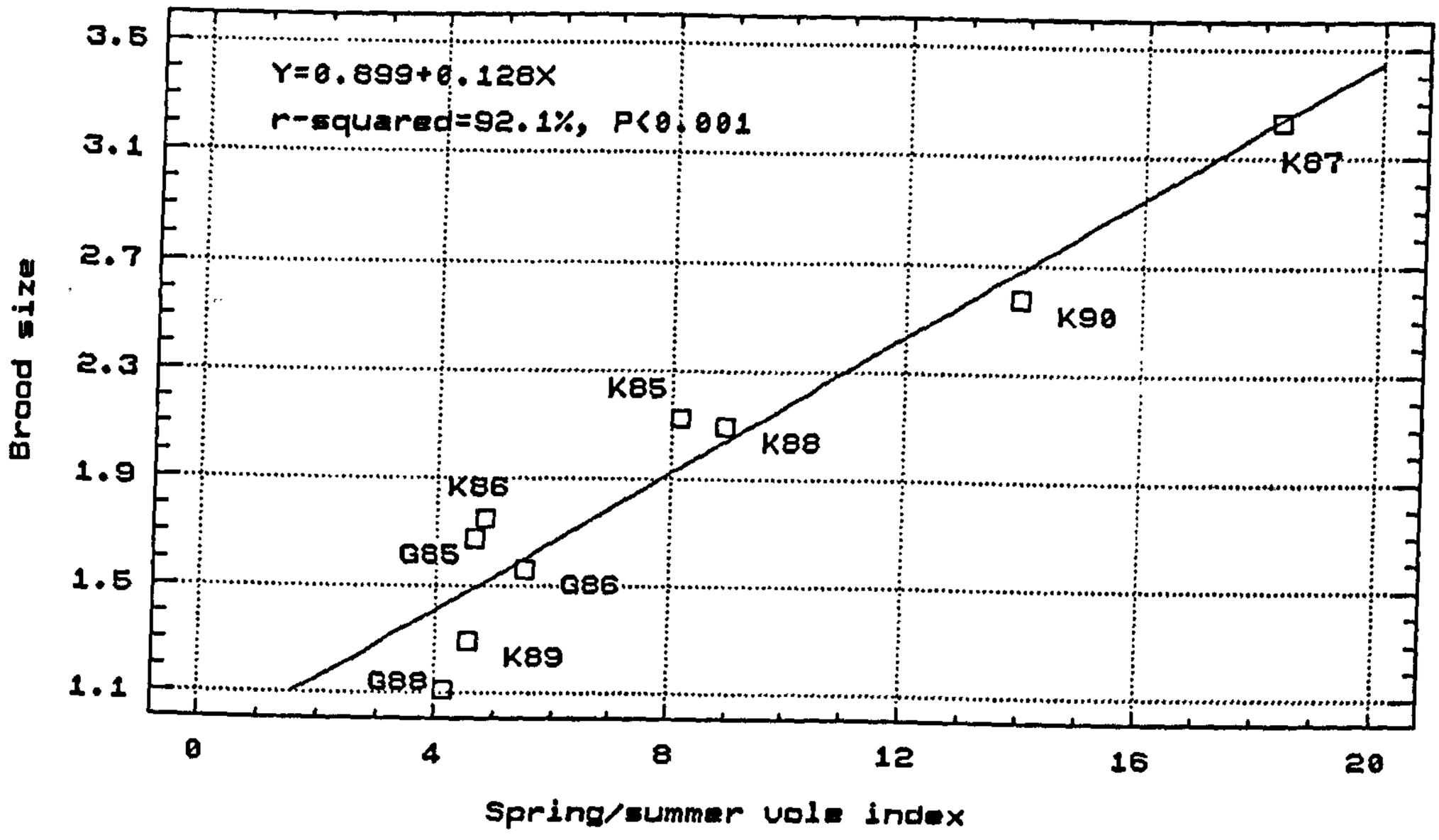


Figure 5.11 Relationship between mean brood size in tawny owls and the mean spring/summer vole index. Each point relates to a study/area year, K = Kielder and G = Glenbranter.

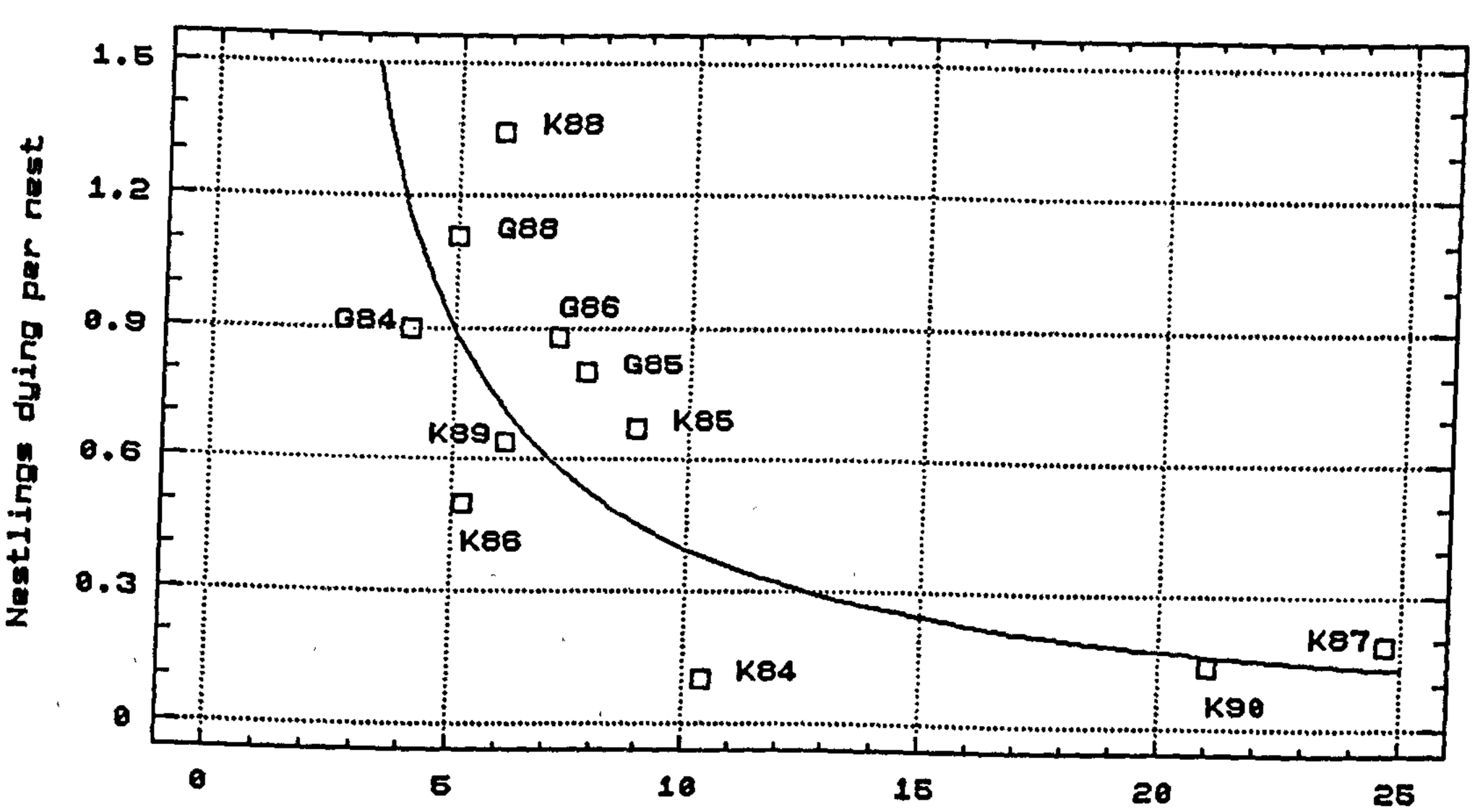


Figure 5.12 Relationship between nestling death in tawny owls (mean number of chicks dying per pair laying) and the mean summer vole index. Each point relates to a study area/year, K = Kielder and G = Glenbranter. The line is fitted by the multiplicative model Y=aX^b, when a=1.790 (equal to Log a) and b=-1.182.

significant between-year variation in nestling mortality in Kielder (Kruskal-Wallis, test statistic = 79.93, P<0.001) but not in Glenbranter (test statistic = 7.92, NS).

To investigate if the loss of chicks was related to vole abundance, the mean number of nestlings dying per pair laying was plotted against the mean PTIs for spring and summer. There was no significant relationship between nestling deaths and spring vole abundance (r=-0.13, n=12, NS), but there was a significant linear relationship with summer vole abundance (r=-0.71, n=11, P<0.05). This relationship appeared to be non-linear and was better when a multiplicative regression model was fitted to the data (Figure 5.12). In this model, summer vole abundance explained 59.6% of variation in nestling mortality while a linear regression explained only 49.9%. This non-linear model suggested that nestling mortality remained constantly low when the May-June PTIs were above 10 but increased rapidly below this point.

Chick mortality was also related to brood size (Table 5.17). In Glenbranter chick mortality increased almost linearly with brood size from 0.1 chicks in broods of one, to 1.4 chicks in broods of four. A similar but much reduced trend was observed in Kielder, from no mortality in broods of one to 0.70 chicks in broods of five.

Mortality rates of individual chicks within broods of different sizes showed a different pattern (Table 5.17). In both study areas chicks in broods of one had the lowest death rate, with only 0-13% dying. In Kielder the greatest percentage of chicks (22%) died in broods of two whereas individual mortality rates were lower (14-16%) in broods of three to five. A similar trend occurred in Glenbranter, with the highest mortality in broods of two and reduced mortality in larger broods. However, mortality rates in Glenbranter were consistently about twice those of Kielder for broods of the same size.

Table 5.17 Mortality of tawny owl chicks in relation to brood size at hatching in Kielder and Glenbranter during 1984-90.

Brood size at hatching	No. broods	No.chicks hatched	No.chicks dying	Mean No. chicks dying per brood	% of chicks dying per brood
Kielder					
1	4	4	0	0.00	0.0
2	54	108	24	0.44	22.2
3	101	303	48	0.48	15.8
4	70	280	40	0.57	14.3
5	10	50	7	0.70	14.0
Overall	239	745	119	0.50	16.0
Glenbranter					
1	8	8	1	0.13	12.50
2	77	154	161	0.79	39.61
3	73	219	76	1.04	36.07
4	8	32	11	1.38	34.38
Overall	166	413	149	0.90	36.08

Table 5.18 Productivity of different clutch sizes of tawny owls in Kielder and Glenbranter during 1984-90.

Clutch size	n	Brood size (SE)	Chicks produced from each egg
Kielder			
1	2	0.00 (0.00)	0.00
2	51	1.29 (0.08)	0.65
3	103	2.45 (0.07)	0.82
4	79	3.25 (0.11)	0.81
5	11	4.27 (0.24)	0.85
6	1	4.00 (0.00)	0.67
Glenbranter			
1	2	0.50 (0.50)	0.50
2	79	1.08 (0.09)	0.54
3	86	1.81 (0.11)	0.60
4	9	2.44 (0.34)	0.61

5.3.4.5 Brood size in relation to clutch size

While brood size increased linearly with clutch size in both study areas (Table 5.18), the number of fledged chicks produced per egg in broods of different sizes, showed an initial increase followed by a tendency to level-off at a clutch size of 3-4 eggs which produced around 0.8 chicks per egg in Kielder and 0.6 chicks per egg in Glenbranter. Clutches of five eggs in Kielder were the exception, but this represented only 11 clutches.

However, in both study areas the individual year models of brood size on clutch size showed a great deal of variation (Table 5.19). At worst, clutch size accounted for 6.4% (Kielder 1982) and 1.3% (Glenbranter 1989) of the variability in brood size, while at best it accounted for 71.7% (Kielder 1984) and 48.2% (Glenbranter 1987). When records from all years were pooled this relationship was better in Kielder (46.2%) than Glenbranter (17.5%) due to much poorer chick survival in Glenbranter.

5.3.5 Condition of breeding adults

5.3.5.1 Comparison between study areas of adult body mass and winglength

Combining study areas and years, female owls were much heavier than males ($t=37.4$, $P<0.001$), with a mean mass of 529 g (n=464) compared to 365 g for males (n=146). There was little overlap, as most females were above 410 g while most males were below (Figure 5.13 upper). Female winglengths were also significantly larger ($t=16.370$, $P<0.001$), with a mean of 266 mm (n=460) compared to 256 mm (n=146) for males, but with much overlap (Figure 5.13 lower).

During 1984-90 females were significantly heavier in Kielder (mean weight 536 g, n=237) than Glenbranter (mean weight 519 g, n=149) ($t=3.28$, $P<0.01$) (Table 5.20). If winglength is taken as an indicator of skeletal size then this difference was not due to females being larger in Kielder. In fact the reverse was true.

Table 5.19 Relationship between clutch size (independent variable) and brood size (dependent variable) in tawny owls by year in Kielder and Glenbranter.

Year	n	Regression equation	r-squared (%)
Kielder			
80	15	Y = -1.727+1.364X	34.09
81	38	Y = -0.400+0.836X	27.43
82	33	Y = 1.019+0.288X	6.36
83	9	Y = -0.625+0.875X	19.14
84	42	Y= - 0.300+0.990X	71.72
85	43	Y = -0.886+1.016X	44.30
86	4	Y = 0.500+0.500X	33.33
87	48	Y = -0.645+1.069X	48.28
88	44	Y = -0.012+0.597X	17.93
89	14	Y = -0.308+0.769X	8.01
90	51	Y = -0.610+1.095X	60.60
80-90	341	Y = -0.463+0.921X	43.82
84-90	245	Y = -0.495+0.948X	46.21
Glenbranter			
84	20	Y = -1.051+0.949X	29.01
85	15	Y = 2.571-0.357X	8.93
86	16	Y = -0.349+0.746X	15.72
87	28	Y = -0.671+1.053X	48.19
88	28	Y = 0.400+0.300X	2.34
89	26	Y = 0.350+0.191X	1.33
90	43	Y = -0.065+0.613X	12.56
84-90	175	Y = -0.329+0.708X	17.53

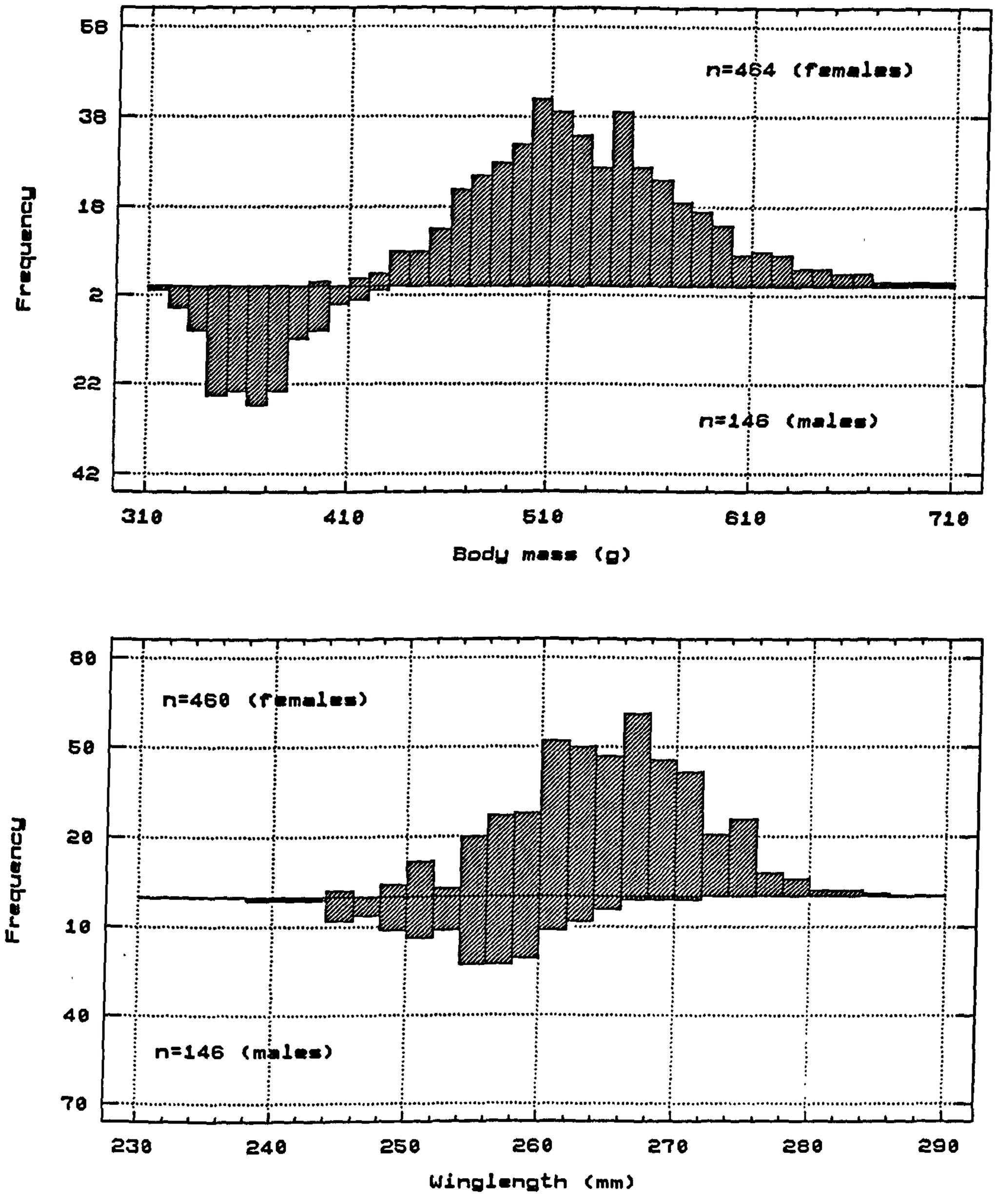


Figure 5.13 Distribution of measurement of body mass in 10 g classes (upper) and winglength in 2 mm classes (lower) of male and female tawny owls combining data from study areas and years.

Table 5.20 Mass and winglength of adult tawny owls caught during the early nestling stage in Kielder and Glenbranter.

Year	Female weight			Female winglength			Male weight			Male winglength		
	Mean	n	SE	Mean	n	SE	Mean	n	SE	Mean	n	SE
Kielder												
80	507.1	13	12.2	263.5	11	2.71	-	-	-	-	-	-
81	556.5	26	10.9	264.9	23	1.30	-	-	-	-	-	-
82	515.0	30	10.4	263.5	30	1.24	-	-	-	-	-	-
83	499.0	9	15.3	264.2	9	3.61	-	-	-	-	-	-
84	537.0	37	8.5	262.2	37	1.14	-	-	-	-	-	-
85	517.2	40	7.5	263.1	42	1.15	-	-	-	-	-	-
86	488.0	4	29.8	267.0	4	3.81	-	-	-	-	-	-
87	578.1	47	8.5	265.1	46	0.93	-	-	-	-	-	-
88	535.8	47	6.7	266.2	48	1.09	364.3	35	3.09	252.4	35	1.10
89	496.5	13	13.1	265.9	13	1.27	361.6	9	6.37	255.0	9	1.31
90	525.5	49	7.2	268.8	48	0.91	365.6	45	3.37	256.0	45	0.69
80-90	533.5	315	3.2	265.0	311	0.40						
84-90	536.1	237	3.6	265.3	238	0.46	364.6	89	2.17	254.5	89	0.60
Glenbranter												
84	510.6	14	10.5	261.1	13	1.36	-	-	-	-	-	-
85	506.3	16	6.2	266.2	17	1.23	-	-	-	-	-	-
86	534.8	13	14.4	265.2	13	1.28	-	-	-	-	-	-
87	521.2	25	7.1	264.2	25	0.88	-	-	-	-	-	-
88	508.3	24	6.9	268.2	23	1.52	357.6	11	2.67	257.5	11	1.39
89	505.2	17	10.0	267.4	18	1.11	365.9	13	5.70	256.8	13	1.29
90	533.1	40	6.0	270.0	40	0.69	367.5	33	4.33	257.6	33	0.98
84-90	519.1	149	3.2	266.8	149	0.47	365.2	57	2.88	257.4	57	0.70

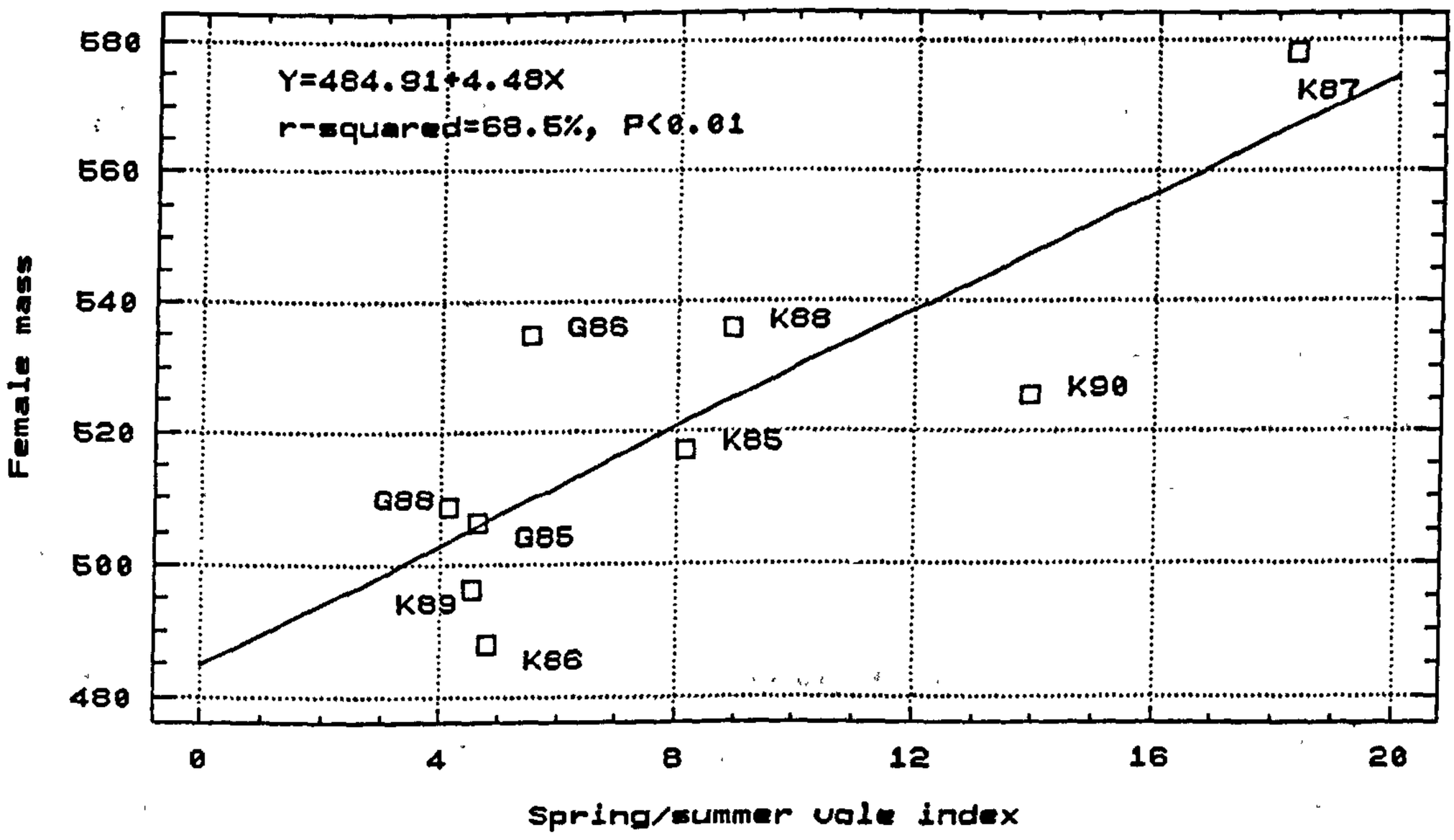


Figure 5.14 Relationship between body mass (g) of female tawny owls and the mean summer/spring vole index. Each point relates to a study/area year, K = Kielder and G = Glenbranter.

Female winglength in Glenbranter at 267 mm (n=149) was significantly larger than Kielder at 265 mm (n=238) (t=-2.10, P<0.05).

In contrast males showed no significant differences in mean body mass between study areas (Kielder 365 g, n=89; Glenbranter 365 g, n=57; t=-0.16, NS) (Table 5.20). However, males also had a significantly larger mean winglength in Glenbranter (Glenbranter 257 mm, n=57; Kielder 254 mm, n-89; t=-3.20, P<0.01).

5.3.5.2 Variation between years in adult body mass

Female body mass varied significantly between years both in Kielder (1980-90, one-way ANOVA F=6.667, df=10,304, P<0.001; 1984-90, F=8.48, df=6,230, P<0.001) and to a lesser but still significant extent in Glenbranter (1984-90, F=2,211, df=7,145, P<0.05). In Kielder mean annual mass ranged from 488 g in 1986 to 578 g in 1987, a range of 90 g. Comparable figures for Glenbranter were 505 g in 1989 to 534 g in 1986, a range of 29 g (Table 5.20).

In both study areas the variation in mean annual body mass of females followed trends in vole abundance. There were significant relationships with spring (r-squared=51.31%, P<0.01) and summer vole indices (r-squared=51.47%, P<0.05), with a point mid-way between these (spring+summer/2) explaining 68.46% of variation in female mass (Figure 5.14).

In contrast to females, males showed no significant variation in body mass between years in either Kielder (one-way ANOVA F=0.150, df=2,86, NS) or Glenbranter (F=0.847, df=2,54, NS). However, fewer years were available for comparisons of male body mass (Table 5.20).

5.3.6 Within-year variation in reproduction

The previous sections (5.3.1-5.3.5) have concentrated on between-year variations in various reproductive parameters of tawny owls.

Much of this variation was related to vole abundance. In this section I explore which factors were related to within-year variation in tawny owl reproduction. The data set was restricted to just two years (1990-1991) in Kielder. This was because I expected male age/experience to influence some of the within-year variation in reproduction, and prior to 1990 I had few data on the males.

In the two years covered, vole populations increased throughout 1990 after a low population in 1989, peaked over the 1990/91 winter and then declined throughout 1991. At any one time, vole populations were not completely synchronized due to a west to east wave-like movement of high populations (Figure 5.15).

First, I calculated Pearson product-moment correlations for; (A) the start of incubation, (B) clutch size, and (C) brood size, using variables associated with vole abundance and body mass, age and breeding experience of the adults (Table 5.21). Each year was treated separately as vole abundance and the age structure of the adults changed between years.

5.3.6.1 Within-year variation in the timing of breeding

The main influences on SIC were negative and differed between the two years. In 1990, vole abundance, particularly during winter, was the main factor related to variation in SIC (Table 5.22). A number of these variables were inter-correlated so to try to clarify the situation a stepwise multiple regression procedure using SIC as the dependent variable and ten independent variables (Table 5.22), selected only autumn vole abundance in the final model (r-squared=14.2%, df=26). None of the other variables added significantly to the fit of this model. The multiple regression procedures used smaller sample sizes in contrast to the individual correlation coefficients because some of the variables had missing data values.

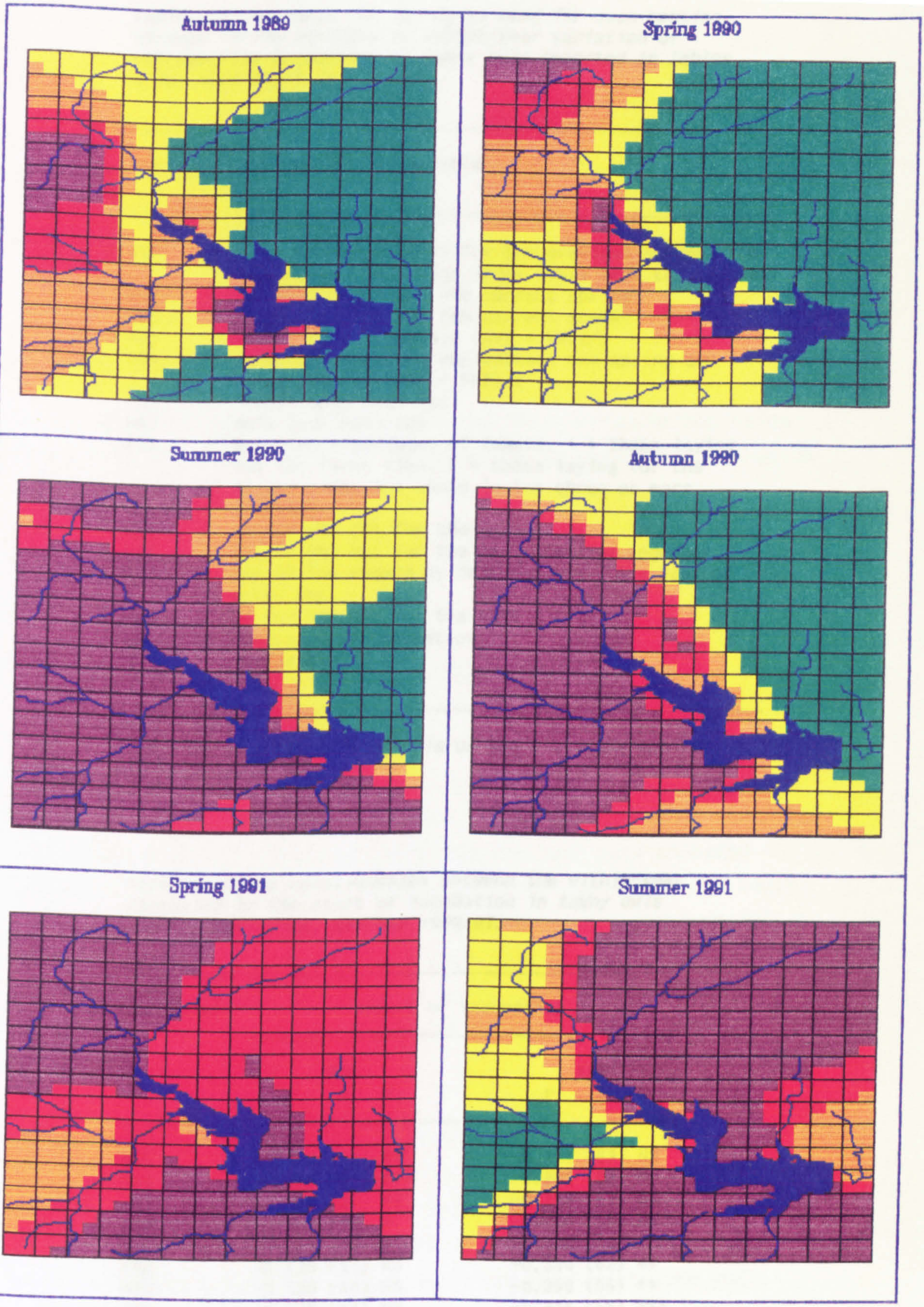


Figure 5.15 Maps showing predicted vole abundance at six assessment dates from autumn 1989 until summer 1991. The algorithm used to produce the maps was a modification of that described by Akima (1978) and uses the seasonal PTI values from 18 vole sign assessment areas (Chapter 3). Predicted vole abundance values (PTIs) are, green <=4.4, yellow 4.5-7.4, orange 7.5-10.4, red 10.5-13.4, purple 13.5>=. The maps predict vole abundance trends in suitable vole habitat throughout the study area. No adjustments have been made for unsuitable vole habitat. Kielder Water is in the centre and each square is 1X1 km.

Table 5.21 Acronyms for variables used for each nesting attempt in the analysis of within-year variation of reproductive parameters of tawny owls reported in Tables 5.22, 5.23 and 5.24.

Acronym	Description of variable
AVI	Vole abundance (PTI) for the previous autumn from the nearest vole sign index (VSI) area to the nest
PVI	As for AVI but for the current spring
SVI	As for AVI but for the current summer
WVI	Winter vole abundance (AVI + PVI)/2
PSVI	Vole abundance mid way between the spring and summer scores (PVI + SVI)/2
FWT	Female body mass (g)
MWT	Male body mass (g)
FBE	Breeding experience of female, 1 = those laying for the first time, 2 = those laying for the second time, 3 = those laying three or more clutches
MBE	As for FBE but for the male
PBE	As for FBE but for the pair breeding together
FAG	Age of the female by calender year, 0 = year of birth etc.
MAG	As for FAG but for the male
SIC	The start of incubation
CLT	Clutch size

See Chapter 3 for more details of the PTI index and VSI areas.

Table 5.22 The relationships between the within-year variation in the start of incubation in tawny owls and ten variables, Kielder 1990-91.

Variables	Start of incubation	
	1990	1991
	r n P	r n P
AVI	-0.407 (51) **	-0.117 (63) NS
WVI	-0.463 (51) ***	-0.201 (63) NS
PVI	-0.392 (51) **	-0.226 (63) NS
FWT	-0.360 (49) *	-0.250 (58) NS
MWT	-0.328 (45) *	-0.038 (50) NS
FBE	-0.135 (51) NS	-0.344 (62) **
MBE	-0.280 (44) NS	-0.398 (55) **
PBE	-0.286 (44) NS	-0.446 (55) ***
FAG	-0.043 (48) NS	-0.338 (45) *
MAG	-0.414 (33) *	-0.393 (44) **

See Table 5.21 for an explanation of the variable acronyms.

In contrast, in 1991 factors associated with the breeding experience and age of the adults explained most of the variation in SIC (Table 5.22). A stepwise multiple regression procedure with the same variables as in 1990, this time selected only breeding experience of the pair in the final model (r-squared=22.98%, df=27).

A stepwise multiple regression with the same variables but using data from the two years first selected winter vole abundance which explained 35.8% of the variation in SIC and second breeding experience of the pairs which increased the r-squared value to 42.6%. No other variable added significantly to the fit of the model.

5.3.6.2 Within-year variation in clutch size

The analyses used were the same as in the previous section but with SIC added. The individual correlations highlighted SIC as the most important influence on clutch size in both years (Table 5.23). There were differences between years in the influences of the other variables. Vole abundance and male age and body mass appeared important in 1990 but not in 1991. Generally there were far fewer significant relationships in 1991 compared to 1990 (Table 5.23). A stepwise multiple regression procedure selected only SIC in the final model for each year and with years together (1990 r-squared=36.82%, df=26; 1991 r-squared=22.33%, df=27; 1990-91, r-squared=39.2%, df=55).

5.3.6.3 Within-year variation in brood size

The analyses were similar to those used in the previous two sections but with clutch size and vole abundance for the spring and summer added. The individual correlations suggested that clutch size and SIC had the most influence on brood size in both years (Table 5.24). Male age also had a significant effect in 1990, as did spring and summer vole abundance and female experience in 1991. In 1990 a stepwise multiple regression procedure selected two

Table 5.23 The relationships between the within-year variation in clutch size in tawny owls and 11 variables, Kielder 1990-91.

Variables	Clutch size	
	1990	1991
	r n P	r n P
AVI	-0.367 (51) **	-0.116 (63) NS
WVI	0.420 (51) **	-0.035 (63) NS
PVI	0.358 (51) **	0.183 (63) NS
FWT	0.261 (49) NS	0.265 (58) *
MWT	0.323 (45) *	-0.161 (50) NS
FBE	0.213 (51) NS	0.234 (62) NS
MBE	0.238 (44) NS	0.252 (55) NS
PBE	0.357 (44) *	0.267 (55) *
FAG	0.150 (40) NS	0.248 (45) NS
MAG	0.553 (33) ***	0.199 (44) NS
SIC	-0.650 (51) ***	-0.617 (63) ***

See Table 5.21 for an explanation of the variable acronyms.

Table 5.24 The relationships between within-year variation in brood size in tawny owls and 13 variables in Kielder, 1990-91.

Variables	Brood size	
	1990	1991
	r n P	r n P
PVI	0.252 (51) NS	0.257 (61) *
SPVI	0.260 (51) NS	0.316 (61) *
SVI	0.195 (51) NS	0.287 (61) *
FWT	0.200 (49) NS	0.195 (58) NS
MWT	0.177 (45) NS	-0/191 (50) NS
FBE	0.072 (51) NS	0.339 (60) **
MBE	0.157 (44) NS	0.207 (54) NS
PBE	0.184 (44) NS	0.143 (54) NS
FAG	0.015 (40) NS	0.271 (43) NS
MAG	0.530 (33) **	-0.023 (44) NS
CLT	0.779 (51) ***	0.680 (61) ***
SIC	-0.591 (51) ***	-0.470 (61) ***

See Table 5.21 for an explanation of the variable acronyms.

variables in the final model. Clutch size by itself explained 55.81% (df=26) of the variation in brood size. This increased to 68.35% (df=25) when summer vole abundance was added. In 1991, clutch size only was selected and this explained 30.76% of the variation in brood size. For the two years combined clutch size and summer vole abundance were again selected (r-squared=44.5%, df=54).

5.3.7 Overall breeding success

This section gives a brief overview of the breeding success of tawny owl pairs in occupied territories. Successful pairs were classed as those owls which fledged at least one chick. Failed pairs were split into four categories, (A) pairs which failed to lay, (B) pairs which failed with eggs, (C) pairs which failed with chicks and (D) pairs which failed due to observer disturbance (section 5.2.5).

A significantly higher proportion of pairs reached the egg laying stage in Glenbranter than in Kielder (1984-90, chi-squared with Yates correction = 4.34, df=1, P<0.05) (Table 5.3). This initial advantage in Glenbranter did not persist through the incubation and nestling stages resulting in chicks being produced in proportionally more occupied territories (Table 5.3). In fact the position was reversed. Proportionally more pairs that laid fledged chicks in Kielder (92.6%) than in Glenbranter (78.9%) (chi-squared with Yates correction = 20.20, df=1, P<0.001). The main reason was that four-times as many pairs failed at the nestling stage in Glenbranter (14.1%) than in Kielder (3.5%). Other failures were also more prevalent at Glenbranter, with almost twice as many nests failing at the egg stage and twice as many nests deserted due to observer disturbance. The level of observer disturbance was similar in both study areas, so the poorer condition of adult females (5.3.5.1) in Glenbranter may have made them more prone to failures, both natural and observer-induced.

Vole abundance appeared to have a similar influence on all aspects of tawny owl reproduction independent of study area. In the regressions of vole abundance in relation to the proportion of pairs laying (Figure 5.3), the start of incubation (Figure 5.6), clutch size (Figure 5.7) and brood size (Figure 5.11), there was no indication that Glenbranter differed greatly from Kielder. In these relationships, the points from Glenbranter fitted around the central portion of the regressions, with the extremes coming largely from Kielder. There were fewer points from Glenbranter in some of these relationships because the measurement of vole abundance was missed in some seasons (Chapter 3). So it would have been difficult to make sense of some of these relationships from Glenbranter alone. Generally, the relationships were little changed with the exclusion of data from Glenbranter (Kielder only), but strengthened with their addition.

5.4. Discussion

5.4.1 Failure to breed

Non-breeding by territory-holding pairs is often difficult to measure in birds, and in tawny owls has only been quantified in some of the most detailed studies. Southern (1970) used graphical *K*-factor analysis to determine which loss or losses from one breeding season to the next had the greatest effect on total annual loss. He concluded that failure to breed was the most important. Smith (1973) reanalysed Southern's data and came to a similar conclusion. Because the incidence of non-breeding appears to be an important aspect of the reproductive performance of the tawny owl, as well as the closely related Ural owl *Strix uralensis* (Lundberg 1981) and other owls dependent on small rodents for food, studies which fail to quantify this aspect of breeding are of limited value (Mikkola 1983 pages 149-152, Percival 1990).

Southern (1970) recorded breeding success in 329 territory/years over a thirteen-year period and recorded no evidence of breeding in 141 territory/years (42.9%). Similarly Delmée *et al.* (1978) in

Belgium showed that non-breeding occurred in 34.1% of 135 territory/years over a 16-year period. Both these studies were in broadleaved woodland.

In my study in coniferous forest, with a larger sample of occupied territory/years, the incidence of non-breeding was much lower, at 28% in Kielder and 21% in Glenbranter (Table 5.3). Southern (1970) inferred that non-breeding was more frequent in years when woodland rodents were scarce in June. However, this seems unlikely unless June rodent densities were correlated with densities in the previous autumn/spring, as the physiological development (or not) of the gonads would need to occur much earlier than June. Indeed, Hirons (1976) showed that in tawny owls a slow ovarian development took place in the autumn. Similar results were obtained by Cavé (1968) working with kestrels.

The present study suggested that fewer frost days in autumn together with high numbers of field voles resulted in more pairs breeding in the subsequent spring. Weather and food availability nearer to the time of breeding appeared to have little obvious effect on whether or not a pair bred. This suggests that tawny owls may be unable to respond to a rapid increase in field voles (or any other prey) in the spring, if the conditions in the previous autumn precluded some initial ovarian development. This view was supported by providing extra food for wild pairs in Glenbranter in 1989 (Petty and Gill in prep). Field vole numbers in the previous autumn through to spring 1989 were low (Chapter 3). Supplemental feeding did not start until after the first pair had started to lay. Then the remaining territories were assigned to twelve pairs matched for similar habitat composition and field vole population levels. From each pair of territories one was selected at random and dead laboratory mice were provided daily in the nestboxes showing the freshest signs of owl activity. Comparing the pairs given extra food with the control pairs showed that there was no significant difference in the proportion of pairs which laid.

5.4.2 The timing of breeding

The timing of breeding in most birds in temperate zones is proximately controlled by daylength (for reviews see Phillips *et al.* 1985; Sturkie 1986). Increasing daylength in the late winter and early spring acts directly on the hypothalamus in the brain to release the hormone gonadotrophin which stimulates gonad growth. Lack (1954) suggested that in each species, breeding was ultimately timed to coincide with peak food abundance at the time when chicks were being fed. Coincidence between breeding and food supply has been confirmed for a number of nocturnal and diurnal raptors. Some of the earliest to breed are species dependant on small mammals, such as the Tengmalm's owl *Aegolius funereus*. Females in Finland start to lay in March and April, just as the snow melts (Korpimäki 1987a). Such an early start ensures that chicks leave the nest well before the growth of ground vegetation makes hunting difficult. In contrast, bird-eating raptors, such as sparrowhawk *Accipiter nisus* and merlin *Falco columbarius*, start breeding much later (in late April and May), so that their chicks are being fed when newly fledged songbirds reach peak abundance in June and July (Newton and Marquiss 1982a; Newton *et al.* 1986a). The Eleonora's falcon *Falco eleonorae* lays even later, in late July and early August. The chicks hatch about a month later and are fed largely on migrant songbirds on their way to winter in Africa (Walter 1979).

As the tawny owl breeds early in the year, it is similar to other raptors which specialise in rodent prey. In my study, in good vole years the peak of laying occurred as early as mid-March. In such years the maximum food requirements fell in early- to mid-May, when nestlings were between half-grown and fledging. In most years this was well before the seasonal peak in small rodent densities, but just before the spring growth of grass which may have made hunting progressively more difficult for the adults. So, as in some other species, the tawny owl breeding season is ultimately timed to coincide with peak food demands of the chicks.

However, a number of other proximate factors act to fine-tune the start of breeding each year (Drent and Daan 1980). Hirons (1976), using his own data and those of Southern (1970), found that in Wytham Wood in Oxfordshire, temperature in February explained 80% of the variation in the annual mean start of breeding in tawny owls, which differed by up to four weeks between-years. Rodent density when incorporated into a multiple regression analysis with the temperature data explained only a further 8% of the variability.

In contrast, my study shows almost the reverse, with rodent density in the winter explaining a very high proportion (90%) of the variation in the annual start of incubation, and weather having no apparent influence. Favourable feeding conditions presumably result in female owls being able to maintain above average body weight throughout the winter, resulting in growth of the follicles.

The mean annual start of incubation varied by about a month in Kielder, but only by 18 days in Glenbranter (Table 5.6). These differences appeared to be a direct result of vole density reaching both higher and lower levels in Kielder than in Glenbranter. Southern's (1970) results from Oxfordshire show an even greater range in the average start of incubation, ranging from 15 March to 21 April, suggesting that rodent densities may have been more variable there.

While much of the between-year variation in the timing of breeding could be satisfactorily explained in my study (largely in terms of food-supply), it was not so easy to explain within-year variation. Only towards the end of the study were enough data available to explore this aspect (Table 5.22). In 1990, winter vole abundance was the single most important factor associated with variation in the start of breeding. The aspect of the pair's experience which was best related to early breeding was age of male. In spring 1990, vole numbers were only just starting to increase after a low in

1989 and there was also much variation in vole abundance within the study area (Figure 5.15). So it was not unexpected that breeding was earlier in those parts of the study area where vole numbers were highest, and that the most experienced males proved able to advance the time of breeding still further, presumably through providing more food for the female.

In the following year the situation was different. Spatial variations in vole abundance appeared to have little direct effect on variation in the timing of breeding. However, in this year vole numbers were at their peak throughout the study area (Figure 5.15). In this situation, the breeding experience of the pair together had the most influence on when incubation commenced. Those males and females who had bred together on three or more occasions laid earliest.

5.4.3 Clutch size

Hirons (1976) analysis of tawny owl clutch size in Wytham Wood suggested that low temperature around the time of laying and low rodent density interacted to depress clutch size. The present study strongly suggests that spring vole abundance was the main influence on the between-year variation in clutch size, with weather having little or no effect.

The significant correlation between mean annual clutch size and the start of incubation was considered an artifact of two other relationships. First, clutch size and the start of incubation both appeared to be independently related to vole abundance. Second, there was a strong seasonal decline in clutch size within-years which differed between years (Table 5.10). Korpimäki and Hakkarainen (1991) also considered that clutch size and laying date in Tengmalm's owl were independently affected by food supply, in contrast to Pietiäinen's (1988a; 1988b) study of the Ural owl and the study of Dutch kestrels (Drent and Daan 1980; Meijer 1988). This is an area of dispute with two schools of thought, with Newton

(Newton and Marquiss 1984), Korpimäki and Petty on one side and the Dutch kestrel workers on the other.

The differences in clutch size between Kielder and Glenbranter and between-years in each study area could largely be explained by variations in spring vole abundance. Mean clutch size in Kielder showed a much greater annual variation than in Glenbranter, again reflecting the higher peaks and lower troughs in the vole population cycles in Kielder. These 'higher' peak years in Kielder resulted in much larger mean clutch sizes and higher mean female weights than Glenbranter, and suggested a causal link between food, female condition and number of eggs laid. The ability of females to replace deserted clutches more readily in Kielder than Glenbranter (section 5.3.3.6) also supported the idea that females were generally in better condition in Kielder. In addition, repeat laying occurred more frequently in good than poor vole years in both study areas, again highlighting the importance of food.

Hirons (1976; 1985a) demonstrated a seasonal decline in clutch size in Wytham Wood, which was also evident in both Glenbranter and Kielder. However, within each of these latter areas, there was much annual variation in when clutches of the same size were laid. More detailed consideration of this within-year variation in Kielder in 1990 and 1991 suggested that in both years the timing of breeding was strongly associated with clutch size. Females laying earliest in the season had the largest clutches. However in 1990 when vole populations were starting to rise, the influence of laying date appeared to be modified by both vole abundance and the age of the male. In contrast, in 1991 when voles were super-abundant in the spring, only the timing of breeding appeared to have a major influence on clutch size.

Hirons (1976; 1985a) analysis of the BTO's Nest Record Data highlighted a very high failure (24.7%) of nests to hatch any chicks. Hirons (1976; 1985a) then went on to suggest that high

desertion rates, particularly of small clutches, may be related to poor provisioning rates by the male. This would result in the female having to hunt more for herself, so leading to eggs chilling and embryos dying. This explanation was not substantiated in my study because the desertion rates during incubation were low, only 4.9% in Kielder and 7.0% in Glenbranter (Table 5.3). One explanation for such a large difference in desertion rates between the two studies, could be that Hirons was unable to control for the effect of observer disturbance from the often scanty information available on Nest Record Cards. I have shown that visits to the nest can cause tawny owls to desert. Over the course of my study this amounted to 13-14% of all nests in each study area, with desertions more likely during egg-laying than later in the nesting period (Table 5.1). In Hirons study such a cause may account for the high desertion rates in clutches of one and two eggs compared to larger clutches.

The tawny owl is potentially a long-lived species so the ability to desert and then relay quickly at another nest site, particularly when relatively little investment had been made in the initial attempt, may well be a strategy that has evolved to increase survival. Once discovered by a potential predator such as pine marten, an owl persisting with a nesting attempt may threaten itself as well as the brood (Sonerud 1985a; 1985b; 1989; Korpimäki 1987b).

5.4.4 Brood size

Lack (1954) suggested that clutch size evolved though natural selection to produce the largest number of chicks that the parents could feed, and that the most frequent clutch size was also the most productive. However, a number of studies have since shown that the most frequent clutch sizes were smaller than the most productive (Klomp 1970; Partridge 1989), and a number of hypotheses have been suggested to explain this discrepancy (Lack 1966; Perrins and Moss 1975; Winkler 1975; Boyce and Perrins 1987; Pettifor *et*

al. 1988; Gustafsson and Sutherland 1988; Partridge 1989; Dijkstra *et al.* 1990 and Dhondt *et al.* 1990).

My study showed a similar difference, in that the most frequent clutch size was three eggs in Kielder and two eggs in Glenbranter (Table 5.7), but most chicks were reared from clutches of five eggs in Kielder and four eggs in Glenbranter (Table 5.18). However, these relationships may well have masked other trends, because there was so much variability in vole numbers between-years particularly in Kielder. To investigate this further, I looked at the relationship between clutch and brood size from 1981 and 1990 in Kielder. During this period each year could be assigned to one of three vole abundance classes, either low, increasing or declining (Table 5.2). In low vole years the most frequent clutch size was two eggs but more chicks were reared from clutches of three eggs (Figure 5.16). There were no clutches larger than three eggs in these years. In both increasing and declining vole abundance years, the modal clutch size was three eggs but most chicks were reared from clutches of five eggs (Figure 5.16). In each of these three, very different types of years, the largest clutch sizes also produced the largest brood sizes. However, using the number of chicks reared from clutches of different sizes may not be the best measure of efficiency of different clutch sizes.

Much energy is used in the creation of eggs, and natural selection may favour those individuals with a high egg to chick ratio. So, I then looked at how many chicks each egg produced in different sized clutches (Figure 5.17). In low and increasing vole abundance years, eggs in the largest clutch sizes (three eggs in low years and five eggs in increasing years) produced most chicks per egg, but in declining vole abundance years the position was reversed. Eggs in the smallest clutches of two eggs were the most efficient at producing chicks and clutches of five eggs were the least efficient.

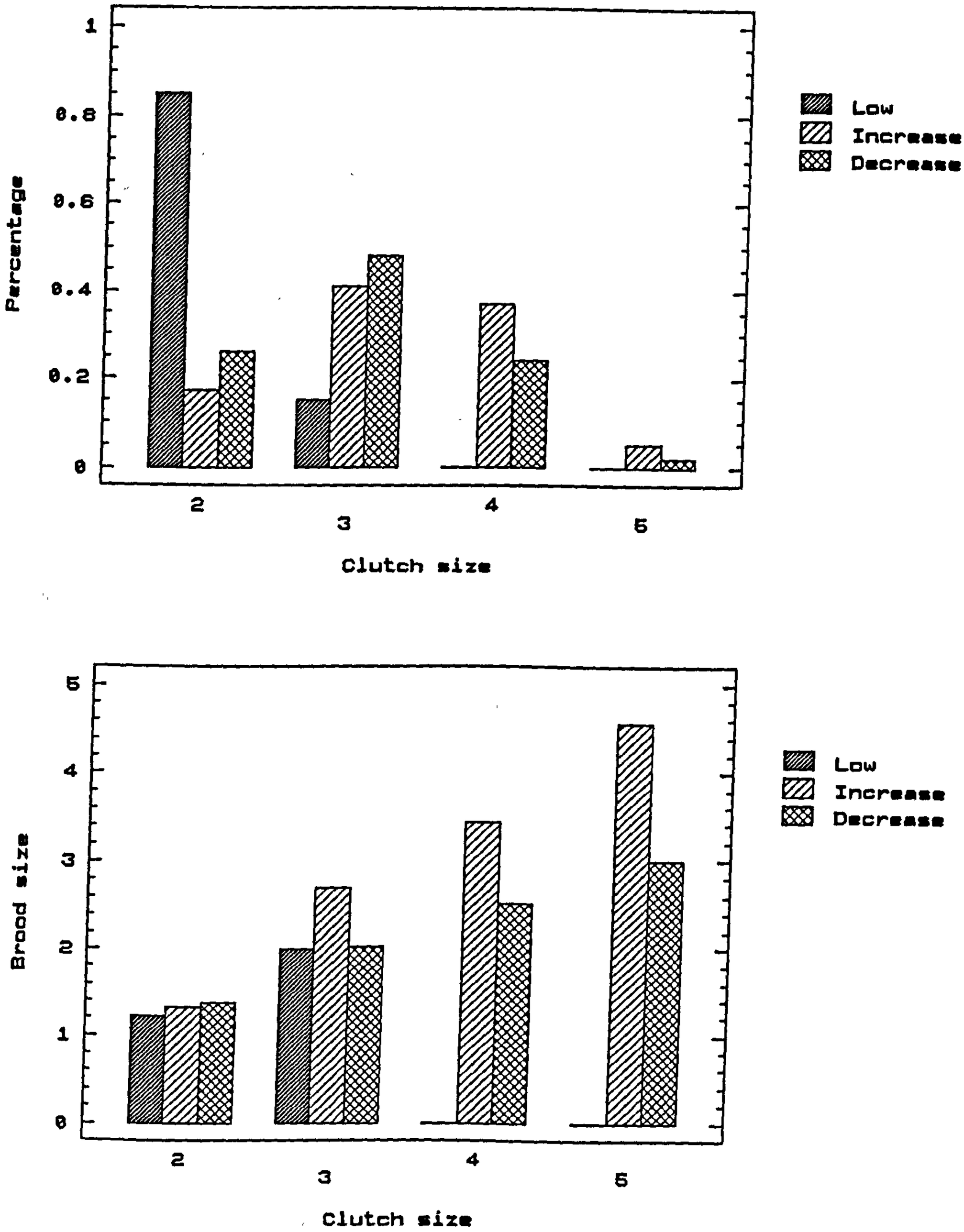


Figure 5.16 The percentage distribution of clutch sizes in tawny owls in three vole abundance classes in Kielder (upper) and mean brood size in relation to clutch size using the same vole abundance classes (lower). Vole abundance classes are; low (1983, 86, and 89), increasing (1981, 84, 87 and 90), and declining (1982, 85 and 88). There were no clutches of four and five eggs in low vole years. Two clutches of two eggs and one clutch of six eggs have been excluded from these figures.

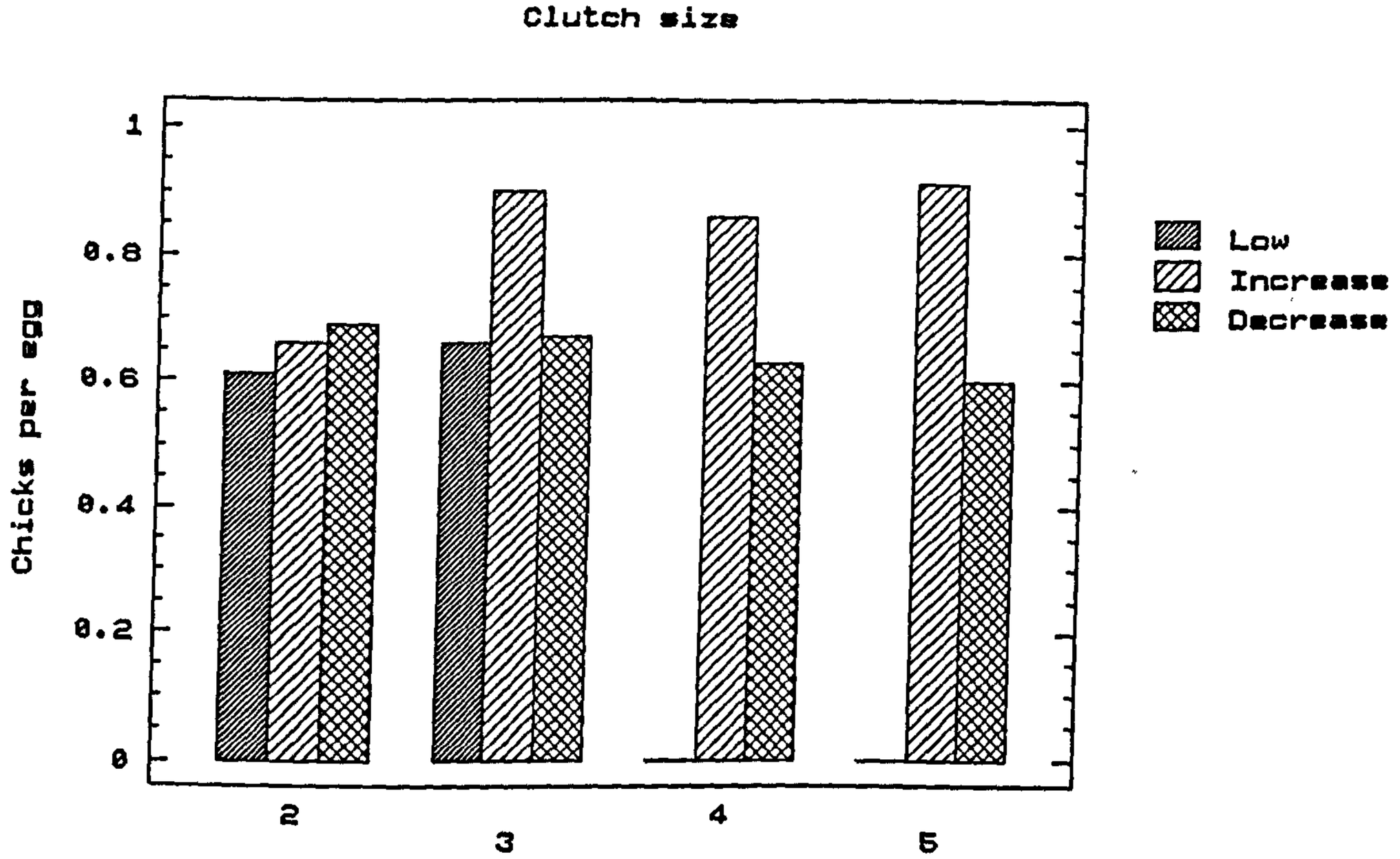


Figure 5.17 The number of chicks produced per egg by clutch size in tawny owls for three vole abundance classes.

Table 5.25 Summary of reproductive data from tawny owls in Kielder and Glenbranter.

Year	No.of occupied territories (a)	% pairs breeding (b)	Mean clutch size (c)	Mean clutch size per territory (d)	Mean brood size per pair laying (e)	Mean brood size per pair (f)	Total chicks produced (g)
Kielder							
80	26	69.2	2.67	1.85	2.00	1.38	36
81	44	93.2	3.17	2.95	2.26	2.11	93
82	42	87.7	2.50	2.19	1.73	1.52	64
83	39	28.2	2.10	0.59	1.22	0.34	13
84	46	93.5	3.44	3.22	3.14	2.94	135
85	50	88.0	2.93	2.58	2.12	1.87	94
86	49	8.2	2.50	0.21	1.75	0.14	7
87	56	85.7	3.63	3.11	3.23	2.77	155
88	61	82.0	3.42	2.80	2.09	1.72	105
89	52	26.9	2.07	0.56	1.29	0.35	18
90	64	84.4	2.90	2.45	2.57	2.17	139
80-90	529	68.6	3.06	2.10	2.38	1.63	862
84-90	378	68.0	3.19	2.17	2.54	1.73	654
Glenbranter							
84	23	87.0	2.90	2.52	1.70	1.48	34
85	25	80.0	2.45	1.96	1.67	1.34	34
86	28	60.7	2.56	1.55	1.56	0.95	27
87	35	85.7	2.55	2.19	2.04	1.75	61
88	40	80.0	2.35	1.88	1.11	0.89	36
89	51	58.8	2.17	1.28	0.77	0.45	23
90	52	88.5	2.80	2.48	1.67	1.48	77
84-90	254	76.7	2.55	1.96	1.50	1.15	292

*(a) and (b) are from Table 5.3; (c) is from Table 5.8; (d) = b*c/100; (e) is from Table 5.16; (f) = b*e/100; (g) = a*f*

Relatively few pairs bred in low vole years, so most offspring are produced during the increasing and declining phases of vole cycles. In these two year types, chick/egg ratios show opposite trends, with clutches of five eggs being the most productive in increasing vole years and clutches of two eggs in declining vole years. The modal clutch size during 1981-1990 of three eggs lay between these extremes. In Chapter 6 I explore how the recruitment of chicks into future generations is influenced by vole abundance.

Southern (1970) and Hirons (1976) showed that in Wytham Wood there was a positive correlation between rodent density in May/June and the size of broods reared by tawny owls. A similar relationship occurred in my study with spring/summer vole abundance explaining 92% of the between-year variability in brood size (Figure 5.11). In contrast, within year variability was strongly related to clutch size, which in 1990 but not 1991 was modified by spring/summer vole abundance. With years combined clutch size had the most influence on brood size but was modified by spring/summer vole abundance mainly through nestlings dying when food was scarce.

Brood size from those pairs laying during 1984-90 averaged 1.4 of a chick more in Kielder than Glenbranter. This difference resulted from clutch sizes being significantly larger (section 5.3.3.1), nestling mortality lower (5.3.4.4) and nest success higher in Kielder (5.3.7). It was difficult to relate this directly to the productivity of the pairs studied by Southern (1970), as his data do not allow the calculation of brood sizes per pair laying. But, it was possible to calculate mean brood size from 331 occupied territory/years at 0.70 chicks. This was considerably lower than the 1.15 chicks per occupied territory/year in Glenbranter and 1.73 chicks in Kielder during 1984-90 (Table 5.25).

5.4.5 Condition of breeding adults

In many birds of prey, the sexes have distinct roles during breeding (Newton 1979; Mikkola 1983). In the tawny owl the male

increasingly provides food for the female by courtship feeding from before egg-laying. As the female's body mass increases, she becomes less effective as a hunter and even more reliant on the male. The female is then dependent on the male for food throughout egg-laying, incubation and for most of the nestling period. Only when the chicks are well feathered does she start to hunt again (Cramp 1985).

Hirons *et al.* (1984) and Hirons (1985a) showed in tawny owls that female body weight increased from late winter to peak at 550-600 g in March around the time of egg laying, and then declined to reach a seasonal low of 450-500 g in August/September. Weights of non-breeding females changed little during the same period, remaining fairly consistent at around 450 g. In contrast, the weights of males fluctuated little throughout the year, remaining at around 350-400 g. Similar seasonal changes in body mass of males and females have been recorded in other owls (Hardy *et al.* 1981b; Korpimäki 1981; 1990; Wijnandts 1984; Exo 1988) and diurnal raptors (Newton *et al.* 1983b; Village 1983). In comparison, relatively little has been published on between-year variation in body mass in raptors (Korpimäki 1990).

To avoid desertions in my study, breeding adults were caught mainly during the period when nestlings were between 5 and 10 days old. Therefore, variations in body weights of both sexes could not be directly related to different stages of the reproductive and annual cycle of tawny owls. However, variation in weights of adults during the nestling period may well give an index of the condition of adults resulting from the cumulative effects of food supply/habitat quality, experience and quality of the adults and reproductive effort during the period before egg-laying until the time of capture.

Male body weight was similar between years in both of my study areas. Presumably males have little opportunity to vary around an

optimum weight. If they put on too much weight they may become less agile and effective at hunting. While at the other extreme if they lose too much weight they risk starvation. Females do very little hunting from the period prior to egg-laying until the neslings are over 15 days so, in contrast to males, they can afford to store both protein and fat. This is primarily to produce eggs but also as insurance against poor provisioning by the male during incubation and the early nestling period. The mean annual body mass of females at the nestling stage showed a range of almost 100 g from 488 g to 578 g, a very large difference for a bird which outside the breeding season weighs between 450 and 500 g (Table 5.20). These differences were positivly related to vole abundance around the time the owls were caught (Figure 5.14). Females in Kielder showed a greater range in annual body mass than Glenbranter, in line with the greater variability in all other reproductive aspects reported in this Chapter.

5.4.6 The effect of weather on reproduction

Vole abundance in both of my study areas explained most of the variation in all aspects of tawny owl reproduction apart from the proportion of pairs laying. Neither rainfall, temperature or the number of days with air frost and snow lying in autumn and winter appeared to influence the timing of breeding or clutch size, nor could weather in spring be shown to have any influence on brood size.

In Chapter 4 the use of nestboxes/holes for roosting was shown to be widespread in broadleaved woodland but unheard of in coniferous forests, suggesting that evergreen habitats provided far more shelter than deciduous ones. Virtually all nesting attempts in my study were in nestboxes which offer considerable protection from cold, wet and windy conditions during the incubating and nestling periods. High rainfall and low temperature have been shown to have detrimental effects of various reproductive parameter of raptors breeding in open nests in temperate regions (see review in Newton

1979). Heavy rainfall is associated with reduced hunting activity, and rainfall and low temperature ensure that incubating or brooding females in open nests have to expend more energy to keep both the eggs/chicks and themselves warm. Nestboxes buffer tawny owls against these effects, and because of this tawny owls may be more productive when breeding in boxes (or dry tree cavities) than in more exposed sites. However, my data from natural sites are too few to make such comparisons.

The shelter provided by conifers may allow male owls to continue hunting in parts of the forest protected from the prevailing weather. Also, the primary food of tawny owls in both of my study areas was the field vole which has both diurnal and nocturnal activity periods (Lehmann 1976; Daan and Slapsema 1979; Lehmann and Halle 1989), unlike the mainly nocturnal wood mice and bank vole in broadleaved forest. This may allow tawny owls to hunt more efficiently during the day when heavy rain prevents hunting at night, so giving them considerably more flexibility than diurnal raptors or tawny owls in broadleaved woodland.

5.5 Summary

1. Variation in the reproductive performance of tawny owls was studied in Kielder Forest, Northumberland (1980-91) and Glenbranter Forest, Argyll (1984-91). The influences of field vole abundance and five weather variables on reproduction were investigated.

2. Overall, significantly more pairs laid in Glenbranter (79%) than in Kielder (72%), but a significantly higher proportion of pairs laying, produced at least one chick in Kielder (92%) than in Glenbranter (79%). This resulted mainly from a higher failure of nests during the nestling stage in Glenbranter. There was a significant negative relationship between the number of days with air frost in autumn and the proportion of pairs laying in the following year. This relationship was modified by autumn vole abundance.

3. The average start of incubation (SIC) was significantly earlier in Kielder (24 March) than in Glenbranter (2 April). There was also significant between-year variation in SIC in both study areas. Vole abundance in the previous winter explained 90% of the between-year variation in SIC.

4. Mean clutch size was significantly larger in Kielder (3.19 eggs) than in Glenbranter (2.55 eggs). There were also significant between-year differences in clutch size in both study areas. Vole abundance in the spring explained 89% of the between-year variation in clutch size.

5. Mean clutch size declined significantly within-years. But between-years there was much variation in the start of incubation for clutches of the same size.

6. The loss of eggs was low, averaging less than a quarter of an egg per clutch. The incidence of unhatched but fully incubated eggs

appeared to occur at random with respect to clutch size, but smaller clutches were more often deserted.

7. Mean brood sizes of pairs laying were significantly larger in Kielder (2.54 chicks) than in Glenbranter (1.50 chicks). Vole abundance mid-way between the spring and summer assessments explained 92% of the variation in brood size.

8. None of the five weather variables used in this study could be shown to have any significant effect on the timing of breeding, clutch size or brood size in tawny owls.

9. Female owls were significantly heavier in Kielder (536 g) than in Glenbranter (519 g), yet no smaller in body size. There were significant between-year variations in mean female body mass in both study areas. Vole abundance mid-way between the spring and summer assessments explained 68% of this annual variation in female weight. Female owls (529 g) were significantly heavier than males (365 g). The weight of male owls did not differ either between study areas or between years in each study area.

CHAPTER 6

POPULATION TURNOVER

6.1 Introduction

Population turnover is the temporal replacement of the breeding population due to mortality, dispersal and recruitment. It is a subject which has received cursory attention in the tawny owl *Strix aluco* and is the least well known aspect in the demography of many bird populations. While much knowledge has been gained on reproduction of birds, it is becoming increasingly obvious that population turnover, which operates largely outside the breeding season, plays an important role in regulating many breeding populations, including raptors (Newton and Marquiss 1986; Newton 1988; Village 1990; Wyllie and Newton 1991). Southern (1970) considered that stability in his breeding population of tawny owls was maintained largely by the rapid replacement of dead adults with juveniles during their first year of life. He postulated that juveniles which were unable to find a territory, starved or moved away.

Information on mortality in British tawny owls comes largely from the recoveries of birds ringed under the National Ringing Scheme, run by the British Trust for Ornithology (BTO) (Southern 1970; Percival 1990). Under this scheme most recoveries come from owls that had been ringed as nestlings and then subsequently reported dead by members of the public. Southern (1970) used life tables (Caughley 1977) to calculate age-specific survival rates from a small number of recoveries from Wytham Wood in Oxfordshire and from the more extensive data of the BTO. Percival (1990) also used the BTO's data, but 20 years after Southern, to calculate both age- and time-specific survival rates (White 1983). There are many problems in the analysis of mortality rates from ring recovery data. Often several of the assumptions involved in the calculation cannot be justified (Newton 1979; Lakhani and Newton 1983; North 1987; Newton 1989). One area of the concern is the assumption that annual mortality becomes constant after a certain age. While this may hold for some birds subject to relatively small annual variations in the quality of their environment, it is unlikely to hold for raptors

feeding largely on microtine rodents with cyclic populations. Another problem is the decline in survival with age (senility) which occurs when not enough time is allowed for all the recoveries to come in.

More realistic estimates of annual loss in the breeding population can often be obtained by ringing individuals, and then recapturing them or their replacements at subsequent breeding attempts (Newton 1979; Newton *et al.* 1983a). Such loss includes both mortality and permanent emigration, but for site-tenacious species such as the tawny owl (Saurola 1987), virtually all the loss is due to mortality. I have used this approach to investigate the population turnover of tawny owls and to demonstrate the major influence of a fluctuating food supply on annual turnover.

6.2 Methods

6.2.1 Identification of individual owls

All nestlings were ringed with a standard BTO ring with a unique number. Nestlings could not be sexed, but birds that were later caught while breeding could confidently be sexed, using weight (Chapter 5, section 5.3.5), the presence or absence of a brood patch and the knowledge that only females incubated and brooded chicks. All breeding adults when caught were checked for rings. Any that were unringed were ringed with the same type of ring used on nestlings.

Very few owls ringed as adults or nestlings were subsequently recovered dead by the public. This is a reflection of the small dispersal distances of both males and females, probably resulting in most deaths occurring inside or around the study area, where there were few people. So the analysis in this chapter is based on recaptures of live birds.

More data were obtained on all aspects of population turnover in Kielder than in Glenbranter. This was because the ringing of adults

and chicks was done over more years (Kielder 1979-1991, Glenbranter 1983-1991) and the population was both larger and more productive in Kielder (Chapter 5). Many aspects of population turnover could not be investigated in Glenbranter due to inadequate sample sizes; so the analysis in this chapter was confined to Kielder where it was also much easier to categorise years according to field vole *Microtus agrestis* abundance (Chapter 5, Table 5.2).

6.2.2 Age determination of adult owls

Many new recruits into the breeding population had been ringed as chicks so their ages were known. Adult owls caught for the first time while breeding and which had not been ringed as chicks, were assigned to one of four age classes on their pattern of primary and secondary feather moult (Petty 1992; Chapter 7); namely, yearling (reared the previous year), two-year-old, three-year-old and three-plus-year-old. This method of age determination was developed during this study and was only available from 1985 (Petty 1992). The method was validated against known-aged ringed individuals and was accurate for all age groups apart from three-year-olds where 23-37% were misclassified by one age class as three-plus-year-olds (Chapter 6). Unringed adult owls caught for the first time during 1979-1984 could not be aged.

6.2.3 Hatchdate of nestlings

The hatchdate was the day when a chick hatched. It was estimated using a winglength/age growth curve (Petty, unpublished data) from the winglength of each chick soon after hatching.

6.2.4 Catching adult owls

Most females were caught at the nest site on each breeding attempt with a butterfly-type net (circular metal support 0.55 m diameter, nylon net 45 mm x 45 mm x 1.5 m, with a 1.5 m bag length) which was mounted on a 2 m long aluminium pole, extendable in 2 m lengths. A few females each year would not leave the nestbox when the net was rattled against it, and these had to be hand-caught. After being

processed, each female was placed back in the box and the hole was blocked for a few minutes to encourage her to settle. Most females stayed in the box once the hole was unblocked.

A sample (n=13) of females was caught for the first time in 1980. These were trapped during the nestling period and none deserted as a result of being caught. In 1981, 20 females were caught while they had eggs, of these six (30%) deserted, apparantly as a result of being caught (Table 6.1). The incidence of desertion was greatest during the first 10 days of incubation. None of the 12 females caught during the nestling stage in 1981 deserted (Table 6.1). In this year vole numbers were increasing, and it seemed possible that the desertion rate would have been higher in declining and poor vole years when the adults would have been

Table 6.1 Nest desertions by female tawny owls resulting from the capture of 32 individuals at different stages during the incubation and the nestling periods in 1981, Kielder.

Reaction of female to capture	Days* when female was caught from the start of incubation (% of total in period)				
	0-10	11-30	31-40	40+	Total
Deserted	5(41.7)	1(12.5)	0(0.0)	0(0.0)	6(0.0)
Did not desert	7(58.3)	7(87.5)	6(100.0)	6(100.0)	26(100.0)
Total	12	8	6	6	32

** Days 0-10 = later stages of egg laying and early incubation*
Days 11-30 = later stages of incubation
Days 31-40 = nestlings <10 days old
Days 40+ = nestlings >10 days old

generally in poorer condition (Chapter 5, section 5.3.5). After 1981 it was decided to restrict catching females to the nestling period, ideally when the youngest chick was 5-10 days old. The errors associated with predicting hatching dates (Chapter 5, Figure 5.1) resulted occasionally in females being caught on eggs, and as expected about 30% deserted. However, most relaid the same year at a new nest site (Chapter 5, Table 5.1).

Male tawny owls proved far more difficult to catch than females. They rarely enter nestboxes, so could not be caught in the same way as females. Only once in many hundreds of successful attempts at catching females was a male also in the nest. Usually the male brings food to the vicinity of the nest site and calls. The female then leaves the nest to collect the food. Two methods of catching males were tried with little success. These included, use of taped calls of male owls set to play at the base of a mist net, and cage traps baited with live house sparrows *Passer domesticus* placed near a nest. Both methods caught very few owls and were time consuming. In 1988, a trap of a similar design to that described by Saurola (1987) (Figure 6.1), was modified to fit the type of nestbox used in this study (Plate 6.1) and used with considerable success thereafter. Eight to ten traps could be operated each night, of which 50-100% would catch males.

The male traps were fixed to the box and set after the female had been caught, processed and put back into the box. If any of the chicks were hungry or in poor condition, two-three dead laboratory mice were also placed in the box. The inner door of the trap prevented the female from leaving the box to collect food. The male was then enticed into the trap by the female responding to his calls and was caught by the outer trap door. The male usually pushed through the inner door and sat quietly with the female and chicks. The trap was left on overnight and then visited as soon as possible next morning. The male was taken from the box by hand, the trap removed and the hole blocked to prevent the female leaving.

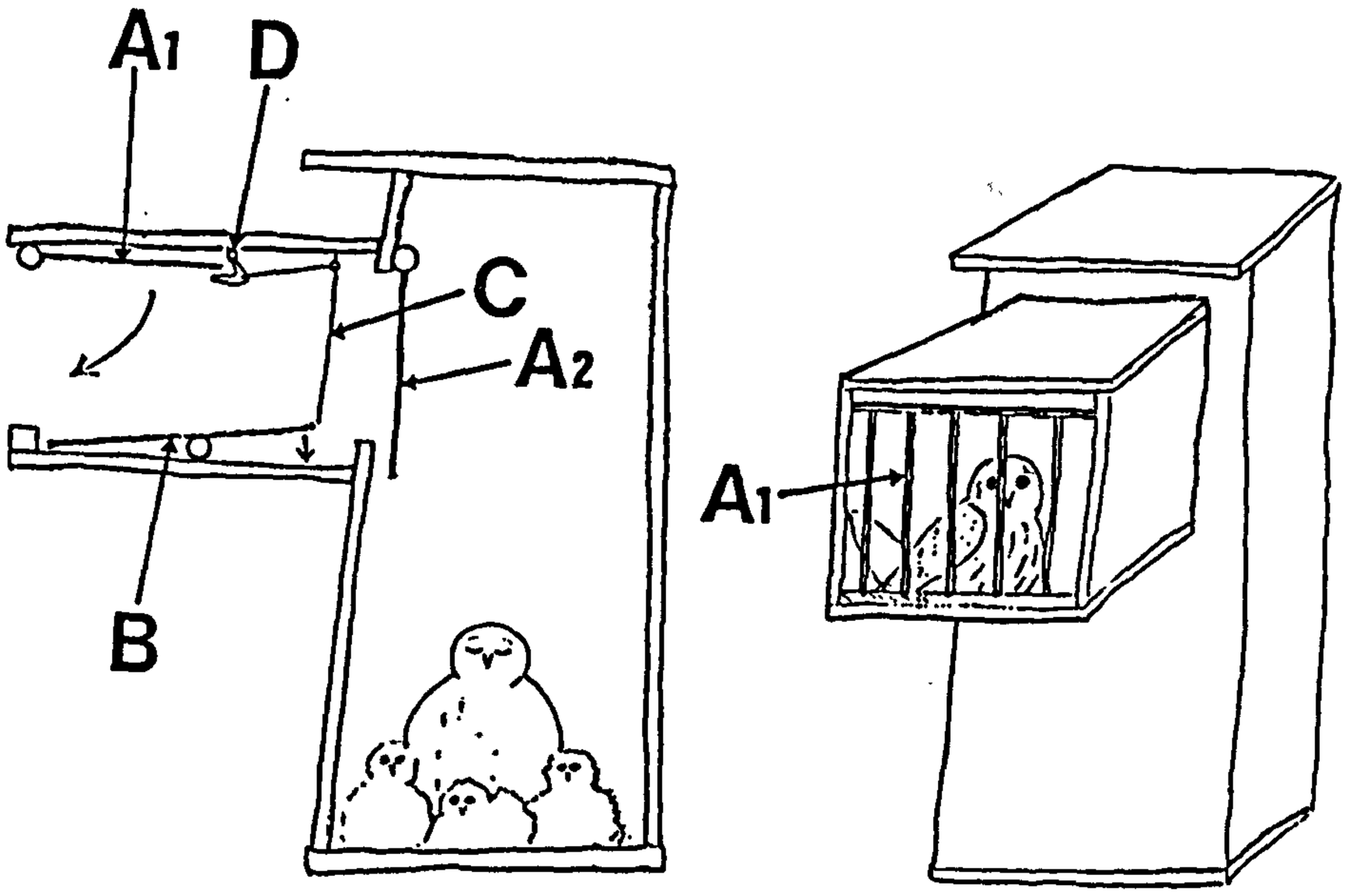


Figure 6.1 A trap for catching male tawny owls which fits over the entrance hole of the nestbox. A1 and A2 are swing doors; B is a swivel board connected by nylon line (c) to a catch on door A1 (from Saurola 1987).

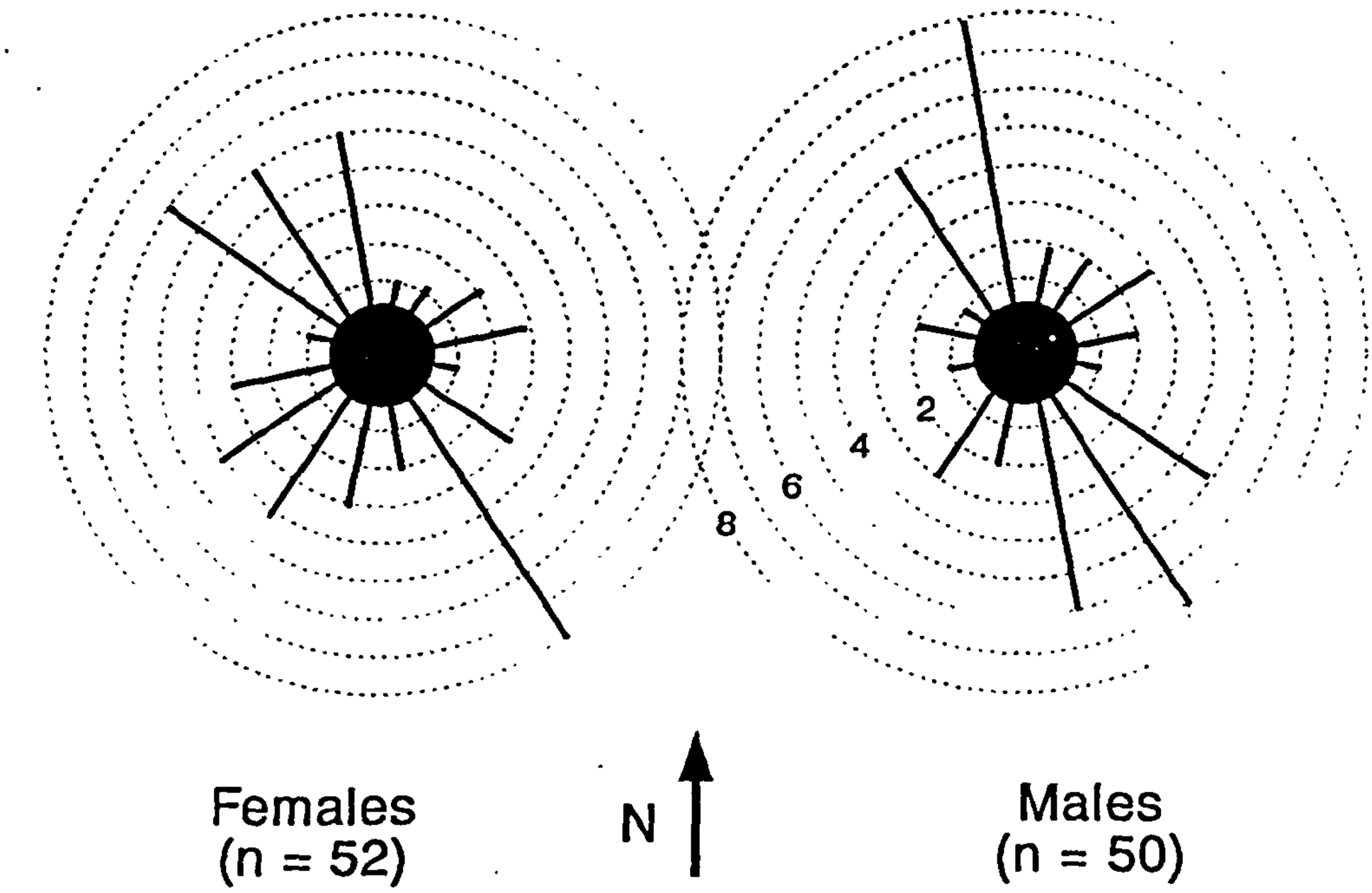


Figure 6.2 Natal dispersal directions of female and male tawny owls in Kielder. Each line is proportional to the number of birds in each 22.5 degree segment of the compass.

Plate 6.1 Male trap on a nestbox.

After processing, he was released, 2-4 laboratory mice were put in the box to compensate for loss of hunting time and the hole was unblocked leaving the female brooding. Five desertions occurred as a result of catching males in 1988, all with chicks <7 days old. In 1989-1991 males were caught when chicks were 8-15 days old, resulting in no desertions.

6.2.5 Food supply

Field voles were the most important food of tawny owls in the study area. Results of assessing vole populations are given in Chapter 3 and Chapter 5. The years 1981-1991 were each assigned to one of three vole year classes, when populations were low, increasing or decreasing (Chapter 5, Table 5.2).

6.2.6 Meteorological data

Meteorological data used in this chapter were taken from the *Monthly Weather Report* published by the Meteorological Office, and referred to Kielder Castle, near the centre of the Kielder study area (Chapter 2). Five montly weather data were used, namely;

A. Mean daily temperature
B. Total rainfall (mm)
C. Number of days with 1.0 mm or more of rain
D. Number of days with snow lying at 09.00 hrs.
E. Number of days with air frost

6.3 Results

6.3.1 Natal dispersal

Natal dispersal was the direction and distance in a straight line that a bird moved from its birthplace to its breeding place. In reality natal dispersal is extremely unlikely to be along the shortest route, but I had no other method of measuring it. In Kielder, 52 females and 50 males ringed as nestlings were subsequently caught as breeding adults within the study area. Most birds settling outside the study area would have been missed (see later).

Dispersal direction of both sexes was similar (Figure 6.2), with a tendency for most birds to disperse in NW-SE corresponding to the alignment of the main valley in the study area (Chapter 2). The treeless hills on either side of the valley appeared to provide a barrier to tawny owls.

In adjacent valley systems on either side of the study area, tawny owls were monitored primarily to look at inter-valley dispersal of females, as males were not caught in these areas. In Kershope Forest to the west 25-30 pairs were monitored during 1987-1991. Most females were caught and all nestlings ringed. None of the females caught in Kershope had been reared in Kielder and none of the chicks reared in Kershope were recovered breeding in Kielder. In Redesdale Forest to the east 10-15 pairs were monitored during the same period with females and nestlings ringed. No owls reared in Redesdale were recovered breeding in Kielder, but one female caught in Redesdale had been ringed in Kielder. This was the only record of a tawny owl moving between valley systems.

Another widely dispersed 20-25 pairs of owls were monitored during 1987-1991 in Wark and Falstone Forests. These areas lay in the same valley system as the study area but 4-10 km down stream. One nestling from this area was subsequently caught as a breeding female in Kielder and three females moved from Kielder to nest within this area.

Within the Kielder study area, the geometric mean dispersal distance was 2.85 km and the median 3.05 km. There was no significant difference between the sexes (Table 6.2). Dispersal distances were positively skewed with the shape of the distribution similar for both sexes (Figure 6.3).

The size of the study area may well have influenced these distributions largely by truncating any long distance movements. However, the skewed distribution suggested that relatively few owls

Table 6.2 Natal dispersal distances in Kielder, excluding birds which moved outside the study area.

Dispersal distance km	Number of tawny owls		
	females	males	both sexes
0 - 0.5	1	1	2
0.5 - 1.0	0	5	5
1.0 - 1.5	5	6	11
1.5 - 2.0	5	4	9
2.0 - 2.5	11	6	17
2.5 - 3.0	4	3	7
3.0 - 3.5	3	3	6
3.5 - 4.0	7	3	10
4.0 - 4.5	6	5	11
4.5 - 5.0	3	6	9
5.0 - 5.5	0	3	3
5.5 - 6.0	2	0	2
6.0 - 6.5	2	1	3
6.5 - 7.0	0	0	0
7.0 - 7.5	0	0	0
7.5 - 8.0	1	1	2
8.0 - 8.5	0	1	1
8.5 - 9.0	0	1	1
9.0 - 9.5	1	1	2
9.5 -10.0	0	0	0
10.0 -10.5	1	0	1
Total	52	50	102
Geometric mean	2.96	2.74	2.85
Median	3.05	3.05	3.05
Variance	1.24	1.20	1.16

There was no significant difference in the mean dispersal distance between the sexes (t-test on data transformed to Log 10, 't=0.594, P>0.05).

Table 6.3 Geometric mean (n) natal dispersal distances (km) of tawny owls in relation to vole year class (from Table 5.33) of hatchyear in Kielder 1981-1991.

Vole year class	Male	Female	Both sexes
Low	4.13 (5)	3.88 (3)	4.04 (8)
Increasing	2.62(37)	2.84(42)	2.73(79)
Declining	2.70 (6)	4.21 (3)	3.13 (9)
ANOVA F =	0.936	0.938	1.43
P =	0.40 (NS)	0.40 (NS)	0.25 (NS)

The one-way ANOVA was performed on dispersal distances transformed to Log 10.

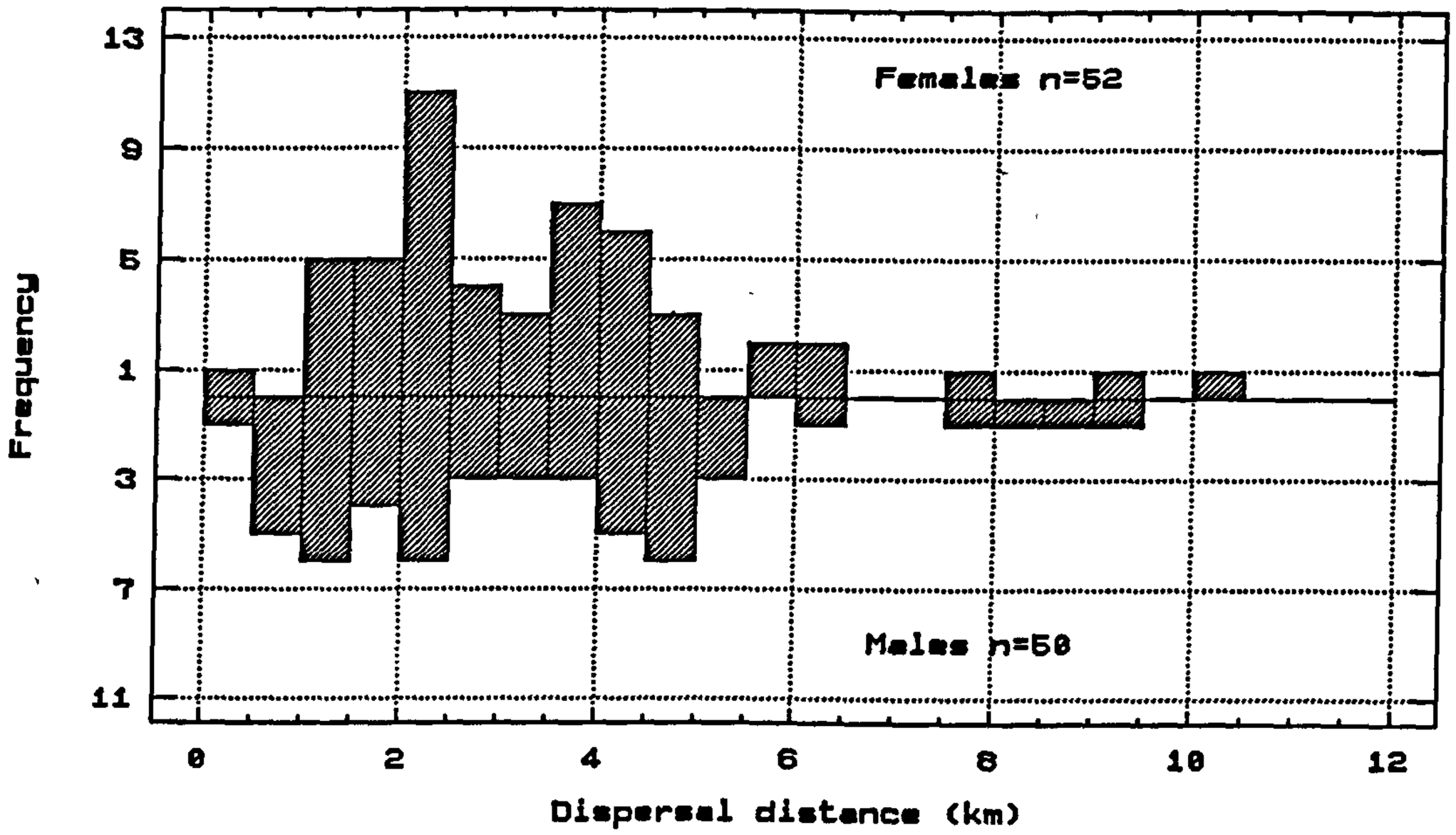


Figure 6.3 Natal dispersal distances of tawny owls in 0.5km classes in Kielder. The upper half of the figure is for females and the lower half for males.

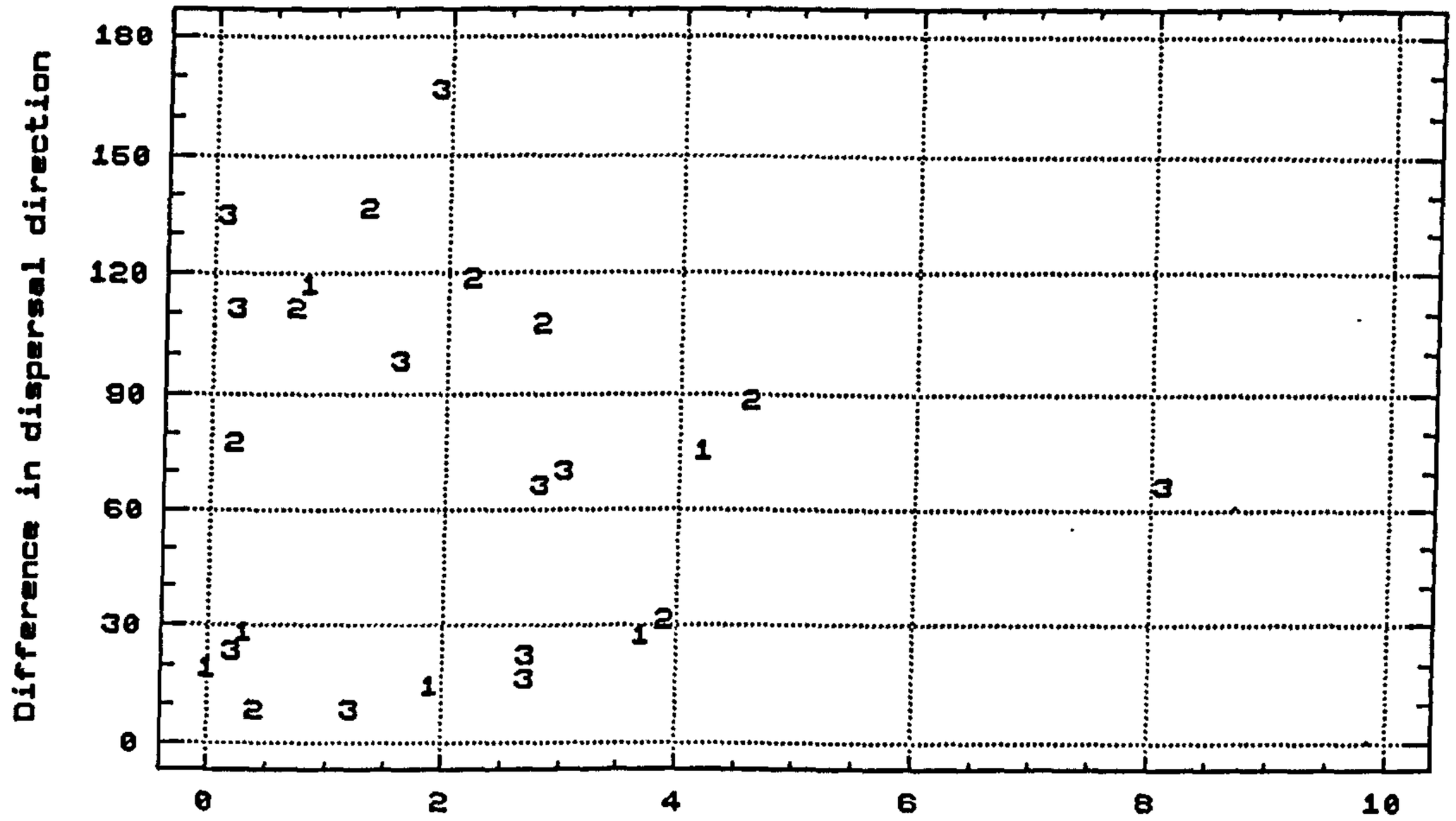


Figure 6.4 Relationship between the difference in natal dispersal distance (km) and natal dispersal direction (degrees) of 25 pairs of siblings born in the same year (1 = both females, 2 = both males, 3 = one of each sex).

would have moved beyond 10 km. This aspect could not be explored further with males because no breeding males were caught in Kershope, Redesdale and Wark/Falstone. However females were caught there, and three which were reared as chicks in the main study area moved 13.7, 16.8, 26.6 km respectively into the Wark/Falstone area. Another female reared in Wark/Falstone moved 13.9 km to breed in the study area. The only inter-valley movement of a female was from a chick reared in Kielder which moved 15.9 km to breed in Redesdale.

It was also possible to investigate whether natal dispersal distances varied in relation to vole abundance in the year of birth (Table 6.3). Both sexes had shorter dispersal distances in years when vole populations were increasing than in years when vole populations were low or declining. However, none of these differences were significant, probably because the samples in low and declining vole years were small.

No birds bred in the territory where they were reared, yet 30% of chicks which were reared within the study area and later bred there settled to breed in either the adjacent territory (eight males and two females) or the next but one (nine males and 12 females).

I also had data on the natal dispersal of 25 pairs of siblings from the same brood to investigate dispersal patterns of closely-related birds. I excluded additional data from siblings born in different years because there was evidence that dispersal distances changed in relation to vole abundance (Table 6.3). I plotted the difference in dispersal direction against the difference in dispersal distance for each pair of siblings (Figure 6.4). This relationship suggested that natal dispersal direction was random as the difference between siblings was evenly spread along the Y axis. The clumping of natal dispersal distance differences at below 5 km (X axis) was a result of most birds dispersing less than 5 km (Figure 6.3). The chance of siblings from the same brood breeding together would have been

greatest when both the X and Y values in Figure 6.4 were near to zero. Only two pairs of male/female siblings settled within 2 km and with less than 30 degrees between each other in these 25 sibling pairs.

6.3.2 Recruitment

In Kielder, 825 ringed chicks fledged in the study area during 1979-1990 (Table 6.4a). Of these, 101 (12.3%) of both sexes had been recruited into the breeding population by 1991. However, because more owls are still likely to be recruited from the 1990 cohort, but not the 1989 cohort (section 6.3.4), it is more realistic to look at recruitment from just the 1979-89 cohorts. Also, these recruitment data for males were not directly comparable with those for females. This was because breeding males were not caught until 1988 whereas most breeding females were caught since 1980. This meant that between 1980 and 1987 some males would have recruited into the breeding population and then died before catching commenced. Therefore, these data underestimate male recruitment. During 1980-1987 (inclusive) nine females had been recruited but were dead by 1988. If a similar number of males went unrecorded, male recruitment during 1979-89 would have been 7.3% instead of 6.1% compared to 7.1% for females or 14.4% with sexes combined. This analysis will also underestimate female recruitment slightly because a small proportion of females that bred only once in the study evaded capture, and some of these may have been ringed as chicks in the study area. The same applies to males but with slightly more birds evading capture. At present, not enough years are available to compare recruitment data between sexes from cohorts where equal effort has been used to subsequently catch breeding adults.

To investigate recruitment in relation to vole abundance, data from 1981 to 1989 only were used. These years spanned three vole cycles, with three years available to assess recruitment from each of the three vole year classes (Table 6.4b). The years 1979-80 were

Table 6.4a The number of chicks ringed and fledging from the Kielder study area by year and vole year class, and the number (%) that were recruited into the breeding population in the study area by 1991.

Year	Vole year class	Chicks ringed (and fledging)	Chicks recruited into the breeding populations		
			female	male	both sexes
79	-	14	1 (7.1)	0 (0.0)	1 (7.1)
80	-	30	2 (6.7)	2 (6.7)	4(13.3)
81	2	86	6 (7.0)	0 (0.0)	6 (7.0)
82	3	57	0 (0.0)	0 (0.0)	0 (0.0)
83	1	11	1 (9.1)	1 (9.1)	2(18.2)
84	2	132	17(12.9)	13 (9.8)	30(22.7)
85	3	92	2 (2.2)	2 (2.2)	4 (4.3)
86	1	7	1(14.3)	1(14.3)	2(28.6)
87	2	155	17(11.0)	17(11.0)	34(21.9)
88	3	92	1 (1.1)	4 (4.3)	5 (5.4)
89	1	18	1 (5.6)	2(11.1)	3(16.7)
90	2	131	2 (1.5)	8 (6.1)	10 (7.6)
79-90		825	51 (6.2)	50 (6.1)	101(12.3)
79-89		694	49 (7.1)	42 (6.1)	91(13.1)

Table 6.4b Summary of the above by vole year class for 1981-1989 (see text).

83,86,89	1	36	3 (8.3)	5(13.9)	8(22.2)
81,84,87	2	373	40(10.7)	29 (7.8)	69(18.5)
82,85,88	3	241	3 (1.2)	6 (2.5)	9 (3.7)
All years		650	46 (7.1)	40 (6.2)	86(13.2)

Vole year classes 1 = low, 2 = increasing and 3 = decreasing vole populations (see Table 5.33).

Table 6.5 Hatchdate of chicks not known to have been recruited into the breeding population compared to those chicks recruited into the breeding populations by vole year class. This analysis uses chicks hatched during 1981-89, in the Kielder study area, and those recruited from these cohorts during 1982-91.

Vole year class	Hatchdate, mean(SE)n		Mann-Whitney U-test
	unrecruited chicks	recruited chicks	
Low	74.4 (1.76) 29	64.8 (4.42) 8	Z=-2.18, P<0.05
Increasing	51.6 (0.62)302	50.0 (1.38)69	Z=-0.99, NS
Declining	51.8 (0.73)230	44.2 (2.37) 9	Z=-2.13, P<0.05

Vole year classes: Low = 1983, 86, 87; Increasing = 1981, 84, 87; Declining = 1982, 85, 88.
Hatchdate = date hatched when 1 = 1 March.

excluded because these years could not be assigned to a vole year class and 1990 because only one year had been available for recruitment. The number of chicks fledging in each cohort was strongly related to field vole abundance (Chapter 5) and ranged between 7 in 1986 and 155 in 1987 (Table 6.4a).

There was also great variation in the recruitment from each cohort. The extremes were 1982 which produced no recruits and 1986 with a recruitment of 29%. This variation appeared to be related to vole abundance (Table 6.4b). Recruitment was highest (22%) from cohorts produced in the low vole years, although only 6% of the 650 chicks were born in these years. Recruitment was similar (19%) from cohorts produced in the increasing vole years, but as 57% of the 650 chicks were produced in these years, many more birds of these cohorts were recruited into future generations. In fact just over 80% of locally recruited adults came from increasing vole year cohorts. There was no significant difference in the recruitment rate between the low and increasing vole year classes (chi-squared with Yates correlation = 0.052, df=1, NS). However, when a similar analysis was done with the declining vole classes added, the difference became very highly significant (chi-squared = 24.23, df=2, $P<0.001$). This was because recruitment from declining vole year cohorts was only 4%. So while many chicks were produced (37% of 650 adults) in these declining vole years, very few survived to breed in the study area. I had no evidence that the low recruitment of these cohorts was caused by a rise in the proportion of birds which dispersed outside the study area (section 6.3.1).

To investigate whether recuitment had changed during this study, a three-point moving average of female recruitment on year was calculated (Figure 6.5). This suggested that recruitment had increased to a peak in 1983-6 and had then declined. However, there was much annual variation and a linear regression fitted to the same data suggested there had been little overall change (b=0.1).

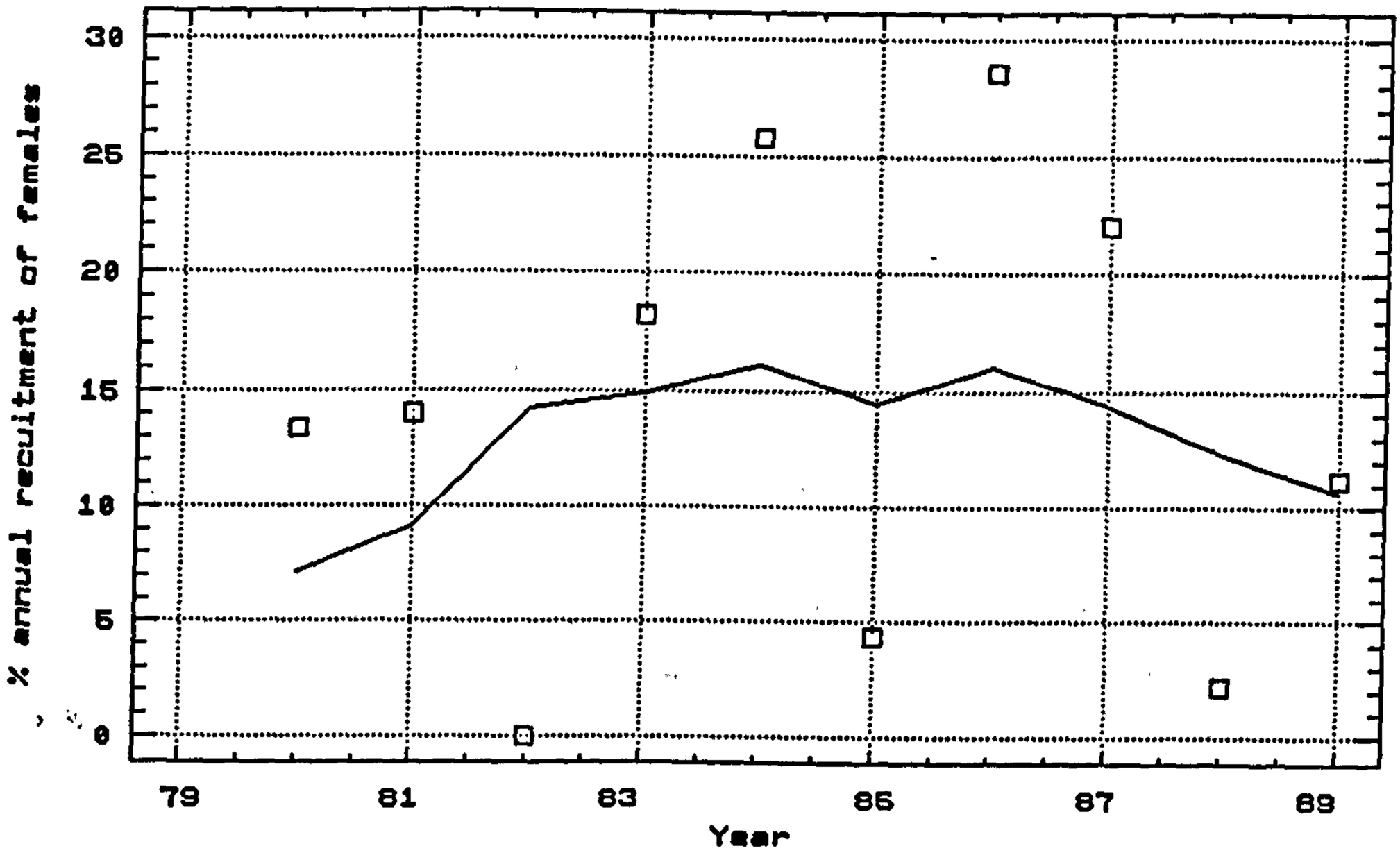


Figure 6.5 A three-point moving average fitted to percentage recruitment of female chicks fledging on birthyear. Female recruitment was calculated from the number of females recruited expressed as a percentage of half the chicks fledging (assuming an equal sex ratio at fledging) (Table 6.4a). The actual data values are also shown.

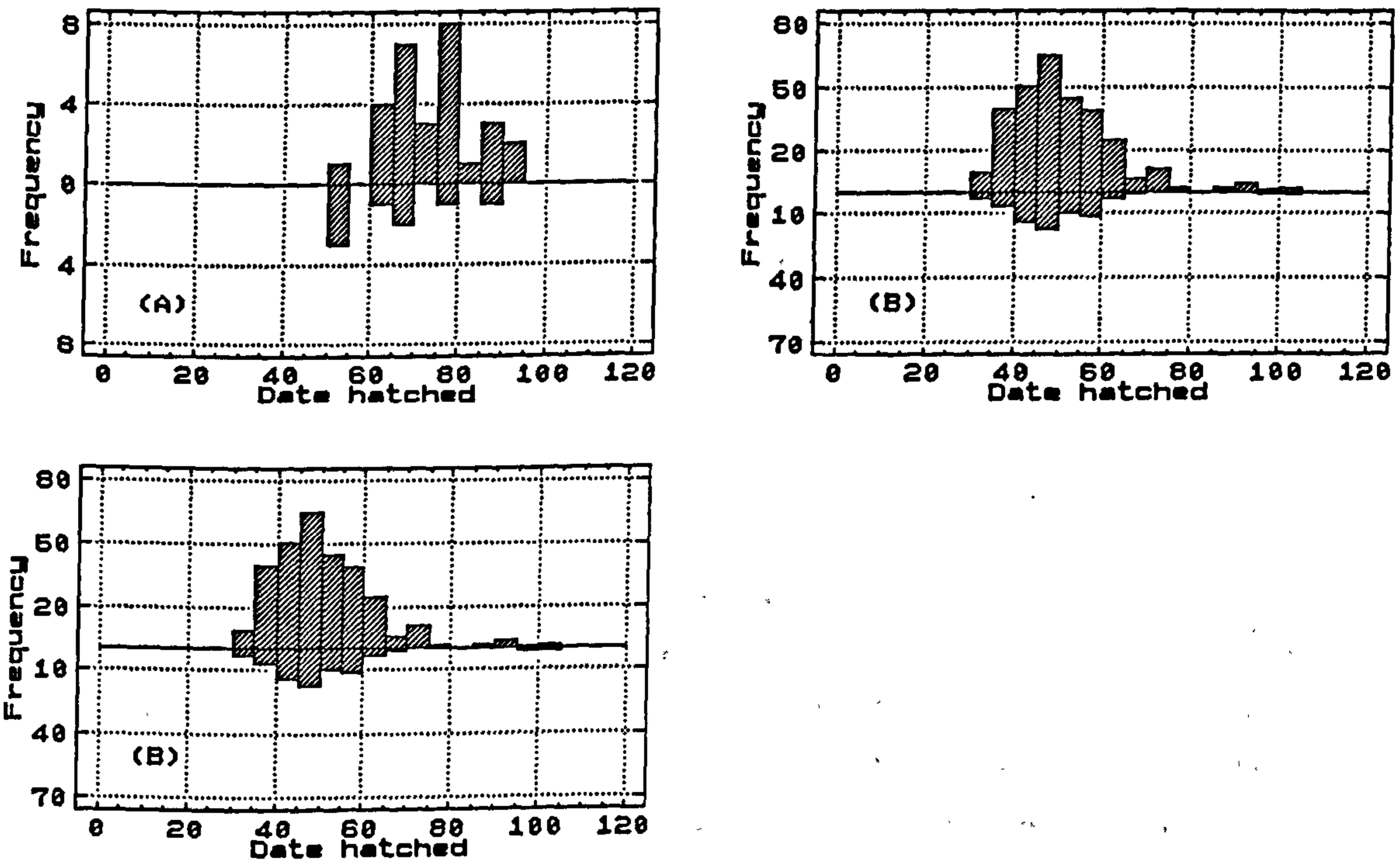


Figure 6.6 Hatchdates (March 1 = 1) in five-day classes of chicks not known to have been recruited into the breeding population (above) and chicks recruited into the breeding population (below), in (A) low vole years (1983, 86, 89), (B) increasing vole years (1981, 84, 87) and declining vole years (1982, 85, 88) in Kielder

It was also of interest to see if hatchdate within these vole year classes affected recruitment (Table 6.5). The hatchdates of chicks recruited into the breeding population were compared to hatchdates of chicks not known to have been recruited. Hatchdates of recruited chicks were significantly earlier in declining and low vole years but not significantly different in increasing vole years.

Hatchdates in low vole years were much later than in the other two vole year classes (Table 6.5) and most survivors came from the earlier nests (Figure 6.6A). During increasing vole years, the distribution of hatchdates of unrecruited chicks compared to recruited chicks were almost identical (Figure 6.6B). Even some very late chicks hatching around day 100 survived. In contrast, in declining vole years none of the chicks hatching after day 60 survived and recruitment was best from earlier hatched chicks (Figure 6.6C). Those hatching between days 35-45 survived best.

It was also possible to investigate how many of the new female recruits into the breeding population came from inside or outside (immigrants) the study area from the ratio of ringed to unringed first-time breeders (Table 6.6a). Only the years 1983-1991 were used, as prior to 1983 the history of most females caught for the first time was unknown. Seventy-four known-aged females were recruited into the breeding population during this period. Forty-five (61%) had been reared in the study area while the 29 (39%) were unringed and assumed to be immigrants.

Most recruitment of females occurred between low and increasing vole years with immigrants comprising 36% of the birds breeding for the first time in increasing vole years (Table 6.6b). Fewer birds were recruited between increasing and declining vole years and even fewer between declining and low vole years. In both of these latter vole year classes immigrants formed 43-45% of the new recruits (Table 6.6b).

Table 6.6a Annual recruitment of female tawny owls reared inside (ringed as chicks) and outside (unringed when first caught) the Kielder study area.

Year	Vole year class	Unknown age and origin		New recruit reared in study area		New recruit reared outside study area	
		first breeding	subsequently breeding	first breeding	subsequent breeding	first breeding	subsequent breeding
79	-	2	0	0	0	0	0
80	-	11	2	0	0	0	0
81	2	23	10	1	0	0	0
82	3	9	26	1	1	0	0
83	1	0	27	3	1	1	0
84	2	1	26	4	4	5	1
85	3	0	24	3	8	4	3
86	1	0	14	0	5	1	4
87	2	2	15	12	5	6	5
88	3	0	16	4	16	2	10
89	1	0	11	1	18	1	7
90	2	0	10	13	18	5	8
91	3	0	10	5	28	4	13
All years		48	191	47	104	29	51

Table 6.6b Summary of the above by vole year classes for 1983-1991 (see text). After 1983 few females were caught in the "unknown age and origin" category.

83,86,89	1	0	52	4	24	3	11
84,87,90	2	3	51	29	27	16	14
85;88,91	3	0	50	12	52	10	26
All years		3	153	45	103	29	51

Vole year classes 1 = low, 2 = increasing and 3 = decreasing vole populations (see Table 5.33).

To investigate if weather conditions during the first autumn (September-November) and winter (December-February) were related to annual variations in the recruitment of females, five weather data (section 6.2.6) from 1983-1991 were used. There were no significant relationships in either autumn or winter.

6.3.3 Mortality prior to first breeding

Recruitment data for females (1981-1989) were also used to estimate a minimum survival between fledging and first breeding (Table 6.4b). An unknown number of females produced in the study area will also have dispersed outside the study area and survived to breed. Discounting these and assuming a sex ratio of unity at fledging, 14.2% of female chicks fledging survived to breed at least once in the study area. Vole-year-specific local recruitment rates were 16.6%, 21.4% and 2.4% for low, increasing and decreasing vole years respectively.

Using the same assumptions, similar figures for males gave overall survival at 12.4% and vole-year-specific local recruitment rates of 27.8%, 15.6% and 5.0% (Table 6.4b). However, as previously explained (section 6.3.2), these figures were likely to underestimate male survival by around 2.4% (1.2%x2). These data suggest that the survival rates of males and females to first breeding in the study area was very similar at around 14.2-14.8%. There was also a suggestion that the mean survival rate of males was lower than that of females in increasing vole years, but higher than that of females in low and declining vole years. However, the sample sizes from low and decreasing vole years were too small to allow a chi-squared test.

6.3.4 Age at first breeding

The definition of first breeding was when eggs were laid for the first time. Many of these first breeding attempts occurred the year after the last occupant was recorded breeding, so it was the first opportunity for these replacement birds to breed unless they had

moved from another territory. However, occasionally it was possible for some birds to have been present but undetected in territories for at least one year before they laid, but I had no way of assessing this. It was possible that a bird may have bred for the first time outside the study area and then moved into the area, but this was unlikely as tawny owls showed a high degree of fidelity to both mate and territory (section 6.3.5). The analysis was first restricted to 86 tawny owls which were ringed as nestlings in the Kielder study area.

Most tawny owls bred for the first time before they were four years old (Table 6.7). The only exceptions were from the 1984 and 1987 cohorts. Both of these years were when vole populations were increasing and many nestlings were reared. From the 1984 cohort one out of 19 (5.3%) and from the 1987 cohort two out of 34 (5.9%) bred for the first time at either four- or five-years of age (Table

Table 6.7 Year of the first breeding attempt by 86 tawny owls (both sexes) in relation to the year they were born. These owls were all ringed as nestlings in the Kielder study area.

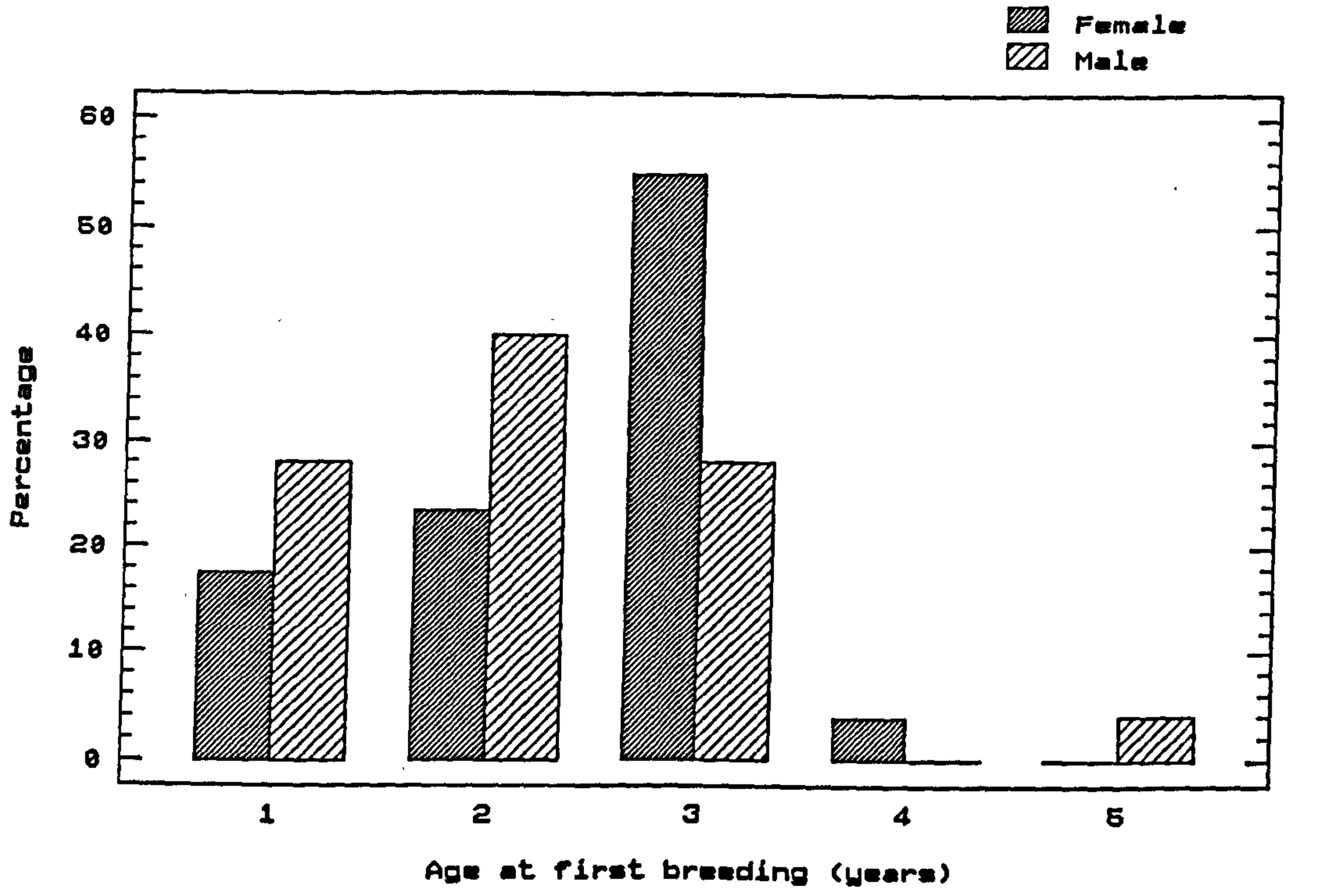
Birth year	Year of first breeding attempt												
	80	81	82	83	84	85	86	87	88	89	90	91	Total
79	0	1	0	0	0	0	0	0	0	0	0	0	1
80	-	0	1	1	0	0	0	0	0	0	0	0	2
81	-	-	0	2	4	0	0	0	0	0	0	0	6
82	-	-	-	0	0	0	0	0	0	0	0	0	0
83	-	-	-	-	1	0	0	0	0	0	0	0	1
84	-	-	-	-	-	5	1	12	0	1	0	0	19
85	-	-	-	-	-	-	0	2	0	0	0	0	2
86	-	-	-	-	-	-	-	0	2	0	0	0	2
87	-	-	-	-	-	-	-	-	9	5	18	2	34
88	-	-	-	-	-	-	-	-	-	0	6	0	6
89	-	-	-	-	-	-	-	-	-	-	1	2	3
90	-	-	-	-	-	-	-	-	-	-	-	10	10
Total	0	1	1	3	5	5	1	14	11	6	25	14	86

6.7). This cohort recruitment analysis suggests that there were unlikely to be any more birds to be recruited into the breeding population from the 1979 to 1988 cohorts. The same is true for 1989 as this was a low vole year with few chicks reared. Already three chicks have been recruited from this cohort, compared to just two and one chick from the previous two low vole year cohorts (1983 and 1986). There were still likely to be recruitable chicks from the 1990 cohort, as this was an increasing vole year with many chicks reared which in the past have shown a high survival to recruitment (Table 6.4b).

For those birds born before 1990, the mean age of first breeding was 2.45 years for females (n=51) and 2.12 years for males (n=25). This difference was not significant (Mann-Whitney U-test, Z=1.89, NS). Most males (40%) bred for the first time as two-year-olds, whereas most females (55%) bred for the first time as three-year-olds (Figure 6.7 upper). These results imply a slightly higher mortality rate in breeding males, thereby creating more vacancies for males to recruit earlier (sections 6.3.6 and 6.3.7). However, there was a difference in the age of first breeding, with sexes combined, in relation to vole year classes (Figure 6.7 lower). Few owls bred for the first time in low vole years and those that did so were mainly two-year-olds. Most owls bred for the first time in increasing vole years, and these were mainly three-year-olds. In contrast, in declining vole years most of the owls that bred were yearlings.

6.3.5 Fidelity to mate and territory

It was only possible to look at mate and territory fidelity from 1988, when males were caught for the first time. In 1988, 36 pairs were caught which were then examined in 1989 for changes in mate and/or territory. In the following two years the original 36 territories were increased, allowing comparisons to be made from 41 territories between 1989 and 1990 and 56 territories between 1990 and 1991 (Table 6.8). Adults were caught at virtually every



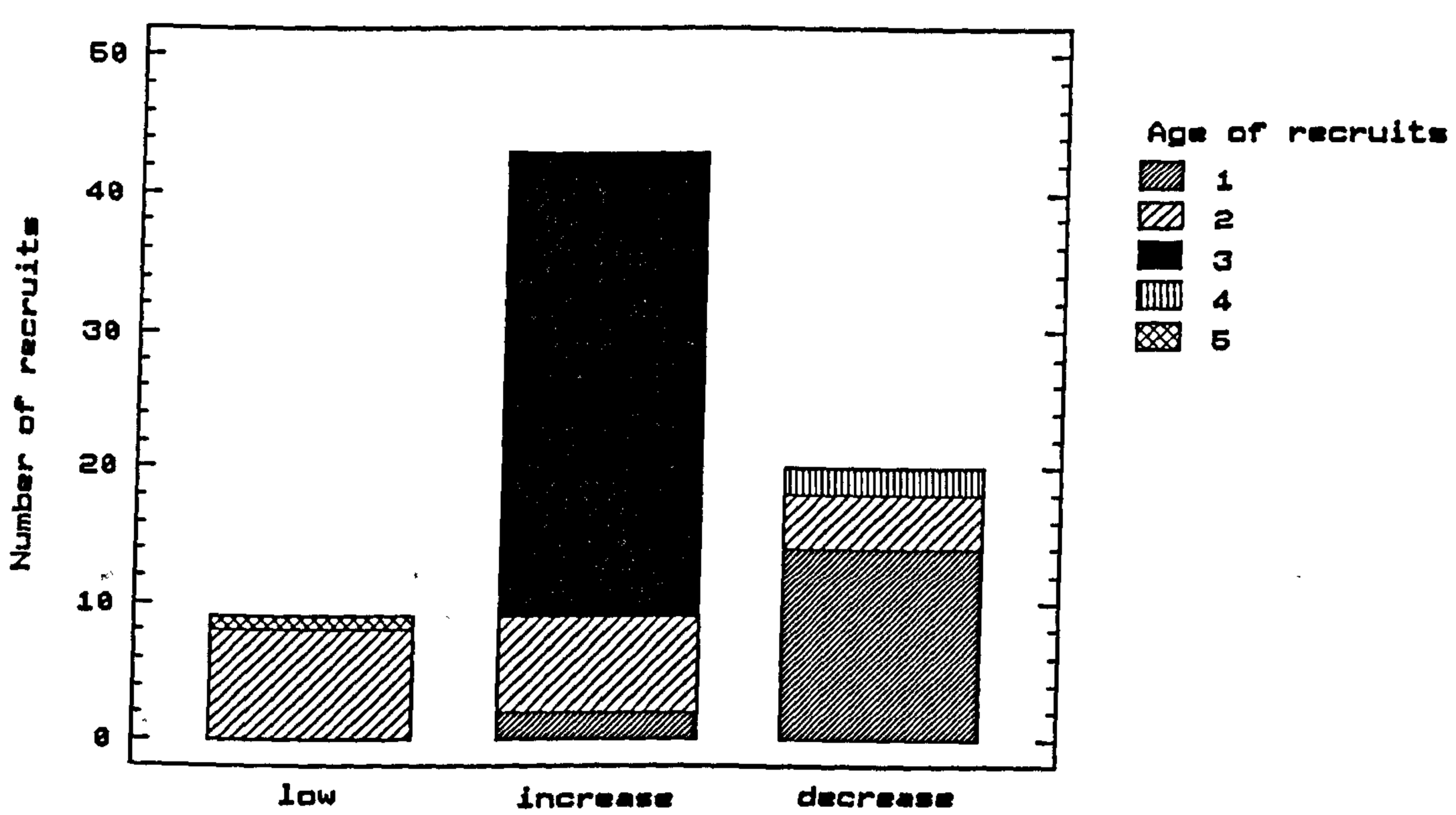


Figure 6.7 Upper - The age of first breeding for male (n=25) and female (n=51) tawny owls. All the owls used in this analysis were ringed as nestlings in the Kielder study area between 1979 and 1989. There was no significant difference between sexes in the proportion of birds breeding at one, two and three-five years of age (chi-squared = 4.84, df=2, NS). Lower - the age of first breeding for 72 tawny owls in relation to vole year class. The owls used in this analysis were ringed in the Kielder study area between 1979 and 1989. The samples were too small in some age/vole year categories to perform a chi-squared test.

Table 6.8 Fidelity of tawny owls to mate and territory. A comparison between three pairs of years in Kielder.

Parameter	1988/89	1989/90	1990/91	overall
A.Number of territories where the pairs were identified	36	41	56	133
B.Same pair (% of A)	20(55.6)	24(58.5)	37(66.1)	81(60.9)
C.Same male, new female (recruit)	0	4	1	5
D.Same male, new female (moved)	1	0	0	1
E.Same male, no female	3	1	0	4
F.Same female, new male (recruit)	2	4	8	14
G.Same female, new male (moved)	0	0	3	3
H.Same female, no male	4	2	0	6
I.New male and female (recruit or moved)	0	4	3	7
J.No male and female	6	2	4	12
Number of territories where one or both adults were missing, E+H+J(% of A)	13(36.1)	5(12.2)	4 (7.1)	22(16.5)
Number of territories where at least one bird was the same, B+C+D+E+F+G+H (% of A)	30(83.3)	35(85.4)	49(87.5)	114(85.7)

New adults; recruit = breeding for the first time, moved = one that has moved from another territory where it bred in the past.

The totals of B to J equal A apart from 1991 (which has one extra) because one of the new birds had also moved from another territory.

I - All were new adults apart from one male in 1991 which had moved from another territory.

Vole populations in 1988/89 were declining/low, in 1989/90 they were low/increasing and in 1990/91 they were increasing/declining.

breeding attempt. In 1989, a low vole year, only eight pairs bred out of the 36 pairs caught in 1988. However, in 1990 most pairs bred again (and were caught) so allowing an estimate to be made of which birds were alive or dead in 1989. In the analysis that follows, a territory often includes more than one nest site (usually a nestbox) used by the same pair in different breeding attempts (Chapter 4).

The results indicate that tawny owls show a very high degree of fidelity to mate and territory (Table 6.8). Overall comparisons between 133 territory years showed that the same pairs were present 81 times (61%) and at least one of the pair was present 114 times (86%). The difference between these two figures was due to birds dying and being replaced by first-time breeders (19 times), where one of the pair was missing (presumed dead) and had not been replaced (10 times), and where birds had moved from another territory where they had previously bred (4 times). In the remaining 19 territory/years (14%) where neither of the original pair were present, seven had new pairs breeding for the first-time and 12 were unoccupied.

Therefore, most of the turnover in the breeding population resulted from the death of the previous occupant/s and its/their replacement with a bird/s breeding for the first time. There was very little movement of birds between territories. In the 133 territory years (or 266 bird years) only one female and 4 males moved, all to adjacent territories. One male moved territory twice, first to a new territory (and new female) and subsequently back to the original territory (and original female). There was sometimes a gap between death and recruitment which either led to the surviving bird staying on its territory without a mate or to the territory becoming temporarily vacant through the death of both occupants.

This overall picture of population turnover was modified by the stage of the vole cycle. The three pairs of years used for

comparison spanned one complete vole cycle, with vole populations declining in 1988, low in 1989, increasing in 1990 and declining in 1991. So the amount of food available for owls between 1988 and 1989 was very low, between 1989 and 1990 it was improved and between 1990 and 1991 it was at its best. Comparing these three pairs of years, the percentage of territories were one or both adults were absent ranged from 36% in 1988/89 to 7% in 1990/91 (Table 6.8). Conversely, the territory occupied by the same pair increased from 55% in 1988/89 to 66% in 1990/91 (Table 6.8). This variation in occupancy resulted from most deaths of adults in 1988/89 and least deaths during 1990/91 (Table 6.8). In 1988/89, six territories were unoccupied and seven had lost one adult. By 1990/91 no territory had just one adult and only 4 were unoccupied (Table 6.8). So, it appeared that first-time breeders were preferentially recruited into single-bird territories rather than to unoccupied ones. In other words a territory with a mate was more attractive than a territory without a mate.

There was no instance of closely-related (parent/offspring or sibling/sibling) pairs breeding together in 48 pairs where the parents of each male and female were known.

6.3.6 Mortality in breeding adults

The calculation of mortality rates was complicated by three factors. First, tawny owls were potentially long-lived. For instance, 13 out of 62 (21%) females caught as breeding adults between 1979-1984 were still alive in 1991. Second, I was unable to determine the age of adult owls caught prior to 1985 (1979-1984) unless they had been ringed as nestlings. Third, I did not catch adult owls every year. This was largely because in low vole years most pairs did not breed (Chapter 5).

During the course of the study (1979-1991) I caught 130 different females in Kielder. Most were then recaught every time they bred until they were replaced by another bird. I assumed that a bird was

dead when it had been replaced, and had not been caught breeding on another territory. A small number of birds did move territory (section 6.3.5) and their history was then followed in the new territory. By checking all the females in the study in consecutive pairs of years and recording whether the female was the same (score 1) or not (score 0), it was possible to calculate minimum survival rates (Table 6.9a). Because many females did not breed and were therefore not caught in the low vole years, I assumed a female was still alive and in the territory in the year she did not breed, providing she was caught in the subsequent year. Sometimes a female was replaced during this two-year period when it was unknown in which year she died. A score of 0.5 was then allocated to each year. This probably underestimates mortality between the declining vole year and low vole year when I would have expected most birds to have died, and overestimates mortality when food supply was improving from a low vole year to an increasing vole year. It would make no difference to overall mortality rates.

Thus calculated, the annual survival rates of females ranged from 96.9% in 1987/88 to 72.8% in 1985/86 (Table 6.9a). Survival rates of males were available for only three years, and ranged from 87.2% to 78.4%. Overall survival rates were 84.3% (SE=2.82%) for males and 85.4% (SE=2.17%) for females, or 87.6% (SE=2.94%) for females when calculated over the same time period as for males. Male and female survival was not significantly different when these three pairs of years were pooled (chi-squared with Yates correction = 0.011, df=2, NS).

The mean expectation of further life can be calculated from the formula (2-m)/2m, when m = the annual mortality expressed as a proportion. This gives mean life expectation of 5.87 years for males and 6.35 years for females, or 7.56 years for females when calculated over the same period as males. This analysis suggests that females did live longer than males but the differences were not significant.

Table 6.9a Survival from one breeding season to the next in male and female tawny owls that bred at least once in Kielder.

Years	Vole year class	No.of adults in first year	Same adults in second year	Survival (%)
(a)	(b)	(c)	(d)	(e)
Female				
79/80	-	2	1.0	-
80/81	-	13	10.5	80.8
81/82	2/3	35	28.5	81.4
82/83	3/1	39	30.5	78.2
83/84	1/2	35	32.5	92.9
84/85	2/3	42	37.0	88.1
85/86	3/1	46	33.5	72.8
86/87	1/2	41	33.5	81.7
87/88	2/3	48	46.5	96.9
88/89	3/1	53	44.0	83.0
89/90	1/2	51	44.0	86.3
90/91	2/3	57	53.0	93.0
Total (female)	-	462	394.5	85.4
Males				
88/89	3/1	37	29.0	78.4
89/90	1/2	39	34.0	87.2
90/91	2/3	48	41.5	86.5
Total (male)	-	124	104.5	84.3

Table 6.9b Summary of the above for females by vole year class from 1981/82 to 1990/91.

	1/2	127	110.0	86.6
	2/3	182	165.0	90.7
	3/1	138	108.0	78.3
All years	-	447	383.0	85.7

*(d) Survival % = d/c*100*
(c) Same adult scores 1, different adult scores 0, when an adult changes during two years and the exact year is not known a score of 0.5 is assigned to each year.

An analysis of female survival in relation to vole year class showed that survival was highest (90.7%) between the years passing from an increasing to decreasing vole population (Table 6.9b), in other words when vole numbers were at their highest through the winter. Female survival was at its lowest (78.3%) between years passing from declining to low vole populations, or when vole numbers reached their lowest level during the winter. In the years when vole populations started to increase (passing from a low to an increasing vole year class) female survival at 87.6% lay between these two extremes.

For females it was possible to investigate whether there had been a trend for survival rates to change with time. First, a linear regression was used with survival as the dependent variable and years as the independent variable (Figure 6.8 upper). The individual points were well scattered due to variability in annual survival related to vole abundance, but there did appear to be a non-significant trend for survival to increase by around 0.9% per year (b=0.88). Second, a three-term moving average was then applied to the same scatter of survival points. This again suggested that female survival had increased during the study (Figure 6.8 lower).

There were no significant relationships between female survival (Table 6.9a) and the five weather variables (section 6.2.6) in autumn and winter during 1980-1991.

6.3.7 Age structure of the breeding population

Most of the breeding birds of both sexes were caught in Kielder in 1990 and 1991, allowing an examination of the age structure of the breeding population. This analysis included adults which had been reared both inside and outside the study area. A high proportion of the breeding adults came from only two cohorts (Figure 6.9). Birds that were three years-old in 1990 and four in 1991 were reared in 1987, while those that were six years-old in 1990 and seven in 1991 were produced in 1984. Both of these years coincided with an

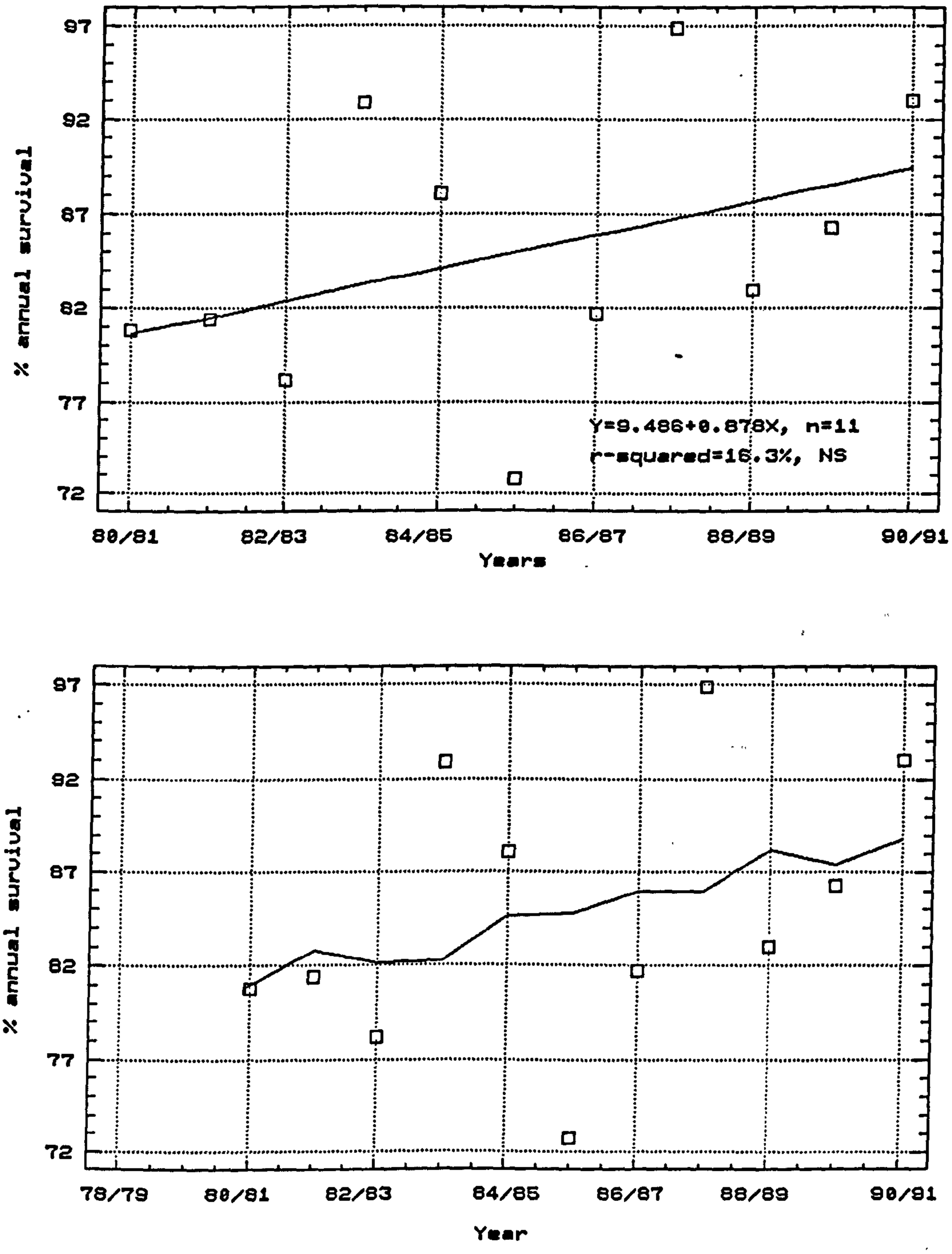


Figure 6.8 Upper - regression of percentage female survival on year (between one breeding season and the next), suggesting an increase in survival of tawny owls during the study in Kielder. Lower - a three-point moving average fitted to the same data.

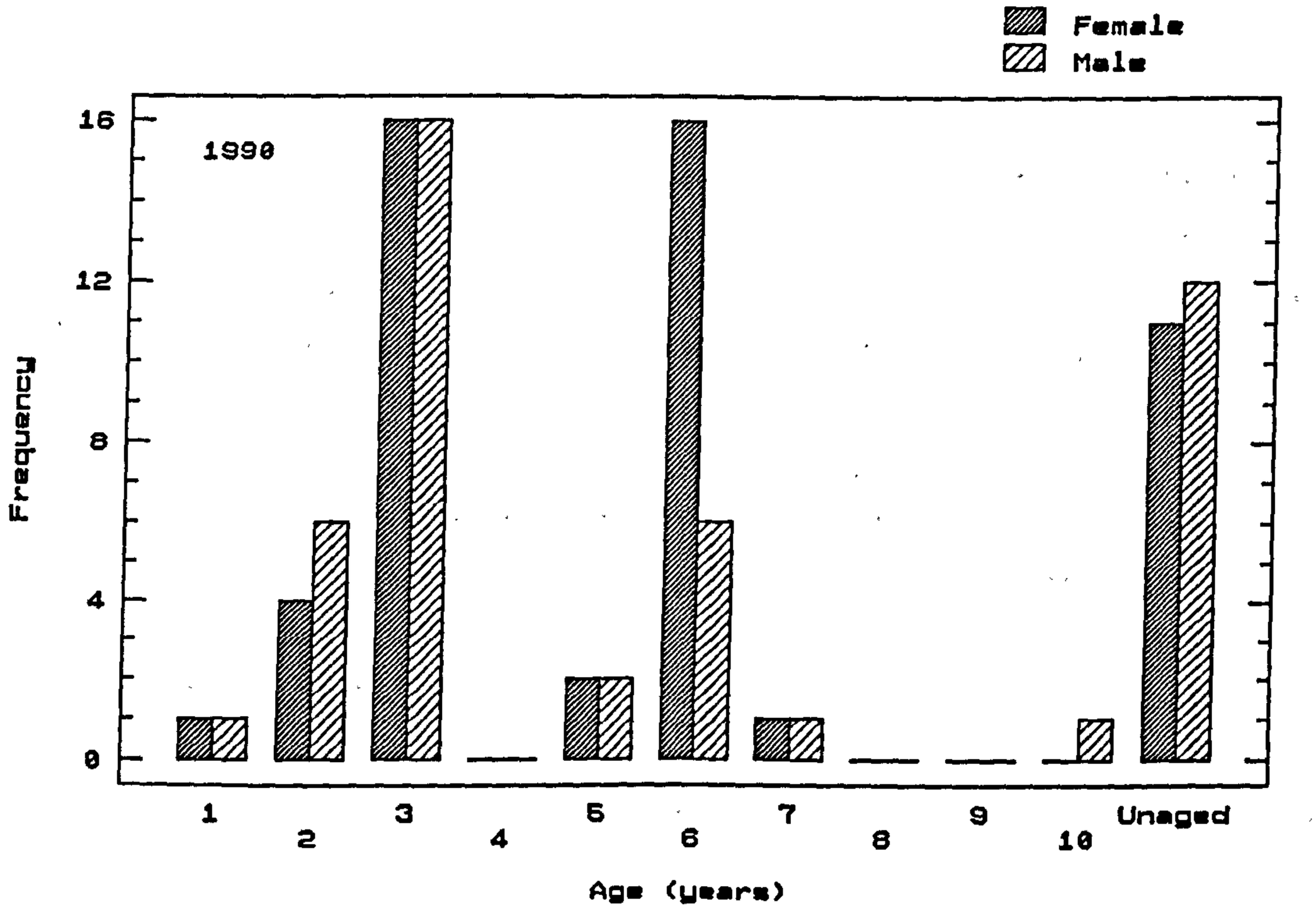


Figure 6.9 Ages of breeding male and female tawny owls in Kielder in 1990 (above) and 1991 (below). The unaged category includes owls caught prior to 1985 when they could not be aged and a few birds caught after 1985 which were four or more years old.

increase phase in the vole population. More yearlings bred in 1991 than in 1990 reflecting both the high productivity of tawny owls in 1990 (Table 6.4a) and high vole numbers over the 1990/91 winter. Of the breeding adults that could be aged, 80% of females and 67% of males in 1990, and 82% of females and 70% of males in 1991, were reared in increasing vole year cohorts. The mean age of females was greater than in males in both 1990 and 1991, and with years combined (Table 6.10). These sex differences in ages were not significant at the 5% level, and were lower than the mean expectation of further life (section 6.3.6). This was because in both years 23.9% of the birds caught could not be aged, mainly because they had been first caught prior to 1985 before a suitable technique to determine age was available (section 6.2.2), or they were four or more years-old when first caught. This unaged category included some birds that were considerably older than the portion of the breeding population that could be accurately aged. For instance, a number of these females were caught for the first time before 1985, some as far back as 1979 and 1980.

Table 6.10 Mean (SE) n age of known-aged male and female tawny owls breeding in Kielder in 1990 and 1991.

Year	Male	Female	Mann-Whitney U-Test
1990	3.76 (0.33) 33	4.25 (0.27) 40	Z=-1.45, NS
1991	4.07 (0.35) 44	4.62 (0.31) 45	Z=-1.35, NS
Overall	3.94 (0.25) 77	4.45 (0.21) 85	Z=-1.88, NS

6.4 Discussion

6.4.1 Natal dispersal

In most species of birds and mammals natal dispersal is sex-biased, with females generally dispersing further in birds and males dispersing further in mammals (Greenwood 1980; Greenwood and Harvey 1982). A number of hypotheses have been suggested to explain the evolutionary basis for such dispersal systems. Inbreeding avoidance may be one, if not the main reason behind sex differences (Pusey 1987; Greenwood 1987). Dispersal *per se* prevents inbreeding between offspring and parents, while differential male-female dispersal prevents inbreeding between siblings. Close inbreeding (between parent/offspring or sibling/sibling) is associated with inbreeding depression (Packer 1979; Greenwood 1980; Falconer 1981; Allendorf and Leary 1986), and Ralls *et al.* (1986) review indicated a very low frequency of close inbreeding in birds and mammals. At the other extreme, outbreeding (between distantly-related populations of the same species) also has a fitness cost (Templeton 1986). So maximum fitness entails a balance between outbreeding and inbreeding.

If inbreeding avoidance is one of the most important ultimate factors influencing natal dispersal, does this apply to tawny owls and if so how does it operate? Only in 48 pairs of tawny owls were the parents of both partners known. There were no cases of closely-related birds breeding together (section 6.3.5). So, on this relatively small sample, inbreeding was avoided, but how?

Greenwood (1980) showed that in birds, females (21 species) were the predominately dispersing sex, but occasionally either males (3 species) dispersed further or there was no difference between the sexes (6 species). The tawny owls in my study fell into the latter category with no significant difference between the sexes. With geometric mean natal dispersal distances of only 2.85 km, thirty percent of birds settled to breed within two territories of the natal territory, although the natal territory was totally avoided

(6.3.1). After leaving the nest, tawny owls remain in their natal territories for 2.5 to 3.0 months during which they appear to be completely dependent on their parents for food (Southern *et al.* 1954; Petty and Thirgood 1989). During this time they have the chance to learn the extent of their parents territory. Southern (1954) and Southern *et al.* (1954) considered that such knowledge would be useful if they subsequently inherited the territory. However, the evidence now presented suggests that such knowledge may allow them to avoid the area from which they were reared. In my study, inbreeding was avoided without sex-biased natal dispersal due largely to avoidance of breeding in the natal territory, siblings from the same brood dispersing in different directions, and breeding owls showing a strong fidelity to their territories. Even when one dies, its mate (either male or female) usually remains in the territory until a new bird is recruited (section 6.3.5).

Wallin *et al.* (1988) provides a detailed study of dispersal in tawny owls in south-west Sweden. Median natal dispersal distances of birds within his study area were 6 km (mean 8.6 km) for females and 5 km (mean 6.9 km) for males. The difference between the sexes was not quite significant. In comparison, the median dispersal distances in my study was only 3.05 km for both sexes (Table 6.2). The differences between these two studies could be related to three factors. First, the size of the study areas; Wallin's area was much larger and may therefore have truncated fewer of the longer distance movements than my smaller area (section 6.3.1 and Chapter 2). Second, the density of tawny owls in the two study areas may have differed, and it may be breeding density rather than distance *per se* that influences natal dispersal (Waser 1985; Buechner 1987). Third, dispersal may be less in relatively continuous nesting habitat than in fragmented landscapes where forests are interspersed with farmland. My study was in the former category but Wallin does not describe his study area.

6.4.2 Recruitment

Tawny owls disperse from their natal territories during August and early September apparently with no aggression from their parents (Petty and Thirgood 1989). Southern (1970) suggested that heavy mortality occurred during the first six months of life. Analysis of BTO data by Hirons (1976) confirmed that most mortality occurred in October and that first-year survival was 56%. A more recent analysis of the BTO data demonstrated that September was the month of peak recorded deaths, closely followed by October, and that survival during the first year of life ranged from 27% to 47% in different parts of Britain (Percival 1990).

My data did not allow the calculation of first-year mortality rates or to pin-point when most mortality occurred. However, it was possible to calculate recruitment rates, and from them minimum survival rates from 825 chicks reared (and ringed) during the study.

Food availability in the autumn/winter following fledging had a major influence on the survival of chicks to first-breeding. The highest survival (22%) was recorded from cohorts reared in years when vole populations were low. These juveniles always went into autumn with a rapidly increasing vole population which remained high throughout the winter (Chapter 5, Table 5.2). So, feeding conditions were favourable after fledging and tawny owl numbers were probably at their lowest level during the three-year vole cycle, thereby reducing competition for food and territories. However, very few young were reared in these low vole years, because prior to the owls' breeding season, vole populations were at their lowest during the three-year cycle resulting in few pairs laying eggs (Chapter 5, Table 5.3). In these low vole years, the few pairs that did breed laid late in the season, and most of the chicks that survived to recruitment came from the earliest nests (Figure 6C). However, a few late-hatched chicks also survived. Therefore, while the survival from these cohorts was good, very few

young were produced (due to few pairs breeding) and consequently they formed a very small proportion of future generations (Figure 6.9).

Similar survival rates (19%) occurred in cohorts reared in years when vole populations were increasing because juveniles then went into a winter with the highest vole populations. A high proportion of the population bred and produced large broods in these years also (Chapter 5, Table 5.25). The result was that a high proportion of future generations came from these cohorts (Figure 6.9). Korpimäki and Lagerström (1988) demonstrated a similar effect with Tengmalm's owls *Aegolius funereus* reared in increasing vole years in Finland. The hatchdate of chicks from these cohorts in Kielder appeared to have little effect on the chance of survival. Even some chicks hatching in June from repeat clutches survived (Figure 6.6B). Presumably this was also a reflection of the good feeding conditions during their first autumn/winter.

In contrast, survival rates were much lower (4%) in decreasing vole years. Vole populations were at their highest through the winter preceeding the breeding season, resulting in a high proportion of pairs laying and fairly large broods being reared (Chapter 5, Table 5.25). However, by the time the chicks fledged, vole populations had already started to crash. By the autumn, vole numbers were at the lowest during the three-year cycle, and remained low throughout the winter. At the time of dispersal in August, tawny owl numbers would also have been at their highest point during the vole cycle. Most territories would have been reoccupied following high adult mortality after the last vole population crash (Table 6.8), and many surviving young from the previous year must still have been in the study area. So juveniles produced in these years, not only dispersed from natal territories when feeding conditions were at their worst, but they also faced competition for food and territories from experienced territorial adults and yearlings from

the previous year's high productivity. So it was not surprising that very few of these young survived.

Unlike young produced in low and increasing vole years, the hatchdate of young from declining vole years also had a strong influence on future survival, with only the earlier hatched chicks recorded as surviving. No chicks hatched as late as May survived (Figure 6C). This was further evidence for the influence of food-supply on juvenile survival. The seasonal decline of vole populations during these types of years meant that chicks which became independent earlier had more time to gain experience before vole numbers reached their lowest point. Deaths probably occurred soon after dispersal from natal territories, or even before.

Petty and Thirgood (1989) studied the ranging behaviour of 12 radio-tagged juvenile tawny owls during the period when they were dependent on their parents, in a year when vole numbers declined through the summer. Five juveniles died within 10 days of fledging, of which three were killed by mammalian predators, one died of disease, and the remaining chick choked while trying to swallow a large field vole. All except the diseased bird were in good condition at death. A further six juveniles died of starvation while still in their natal territories but much later, between 30 and 80 days post-fledging. Only one (8%) of these radio-tagged juveniles became independent. In contrast, Southern (1970) and Hirons (1976) both reported very low mortality during the period when young were dependent on their parents, only 1.7% (4 out of 231 chicks) and 2.9% (1 out of 34 chicks) respectively, based on locating and monitoring broods from the persistant calls of the juveniles (Muir 1954; Southern *et al.* 1954). However, these counts of fledged young appear to have been undertaken in the third week of July when the young would have been out of the nest 60 days or less. Petty and Thirgood (1989) showed that most deaths from starvation occurred after 70 days from fledging, near the time when dispersal was expected.

6.4.3 Age at first breeding

Virtually all tawny owls at Kielder started to breed before they were four-years-old. What was unexpected, was the number of males that bred for the first time as yearlings, rather than at two- or three-years of age. In owls and most species of true hawks, there are quite separate roles for each sex during the breeding season (Newton 1979; Mikkola 1983). The male is the hunter while the female incubates and tends the young. Females do virtually no hunting from prior to egg-laying until the nestlings are well feathered. Time is necessary to gain experience to hunt efficiently and so provide for a female and family. In some raptors this results in males rarely breeding as yearlings. Martin (1986) suggested that tawny owls needed to learn the geography of their territory extremely well to be able to hunt efficiently at night, with eyesight and hearing not dramatically better than in humans (Chapter 1). This too suggests that it would be advantageous for tawny owls to defer breeding, particularly for males. However, in Kielder there were unoccupied territories in every year of the study (Chapter 4) which may have encouraged males to breed earlier than in populations with few vacant territories and many non-breeding floaters of an older age. Males could also have recruited earlier in Kielder because mortality in breeding males was slightly higher than female, thereby creating more vacancies.

These recruitment data for Kielder show that at certain stages in the three-year vole cycle, there must be surplus, non-territorial owls within the Kielder study area (Figure 6.7 lower). I have shown that owls recruited into the breeding population were mostly reared in years when vole populations are increasing (Table 6.4b). In these increasing vole years most first-time breeders were three-year olds, having been produced in the increase phase of the previous vole cycle (Figure 6.7 lower). However, in the following year (declining vole years) most recruitment came from owls reared in the previous year, strongly suggesting that there were few older birds left in the non-breeding sector. It also indicated that a

lack of older surplus birds in the previous year (increasing vole years) may actually have restricted the size of the breeding population in what was potentially the most productive year because there were still vacant territories. This apparent shortage of birds was not compensated by immigration (Table 6.6b), because immigrants then formed a lower proportion of new recruits than in low and declining vole years. This contrasted with declining vole year classes when, although the breeding population did increase due to the recruitment of yearlings, there were also many other yearlings which did not breed. These remained in the study area to be recruited after the low phase in the vole cycle. Southern's (1970) study in lowland broadleaved woodland suggested a quite different recruitment system. After the breeding season, independent juveniles were quickly recruited into vacant territories, and those without a territory died from starvation, although little evidence was provided to substantiate this.

6.4.4 Survival

Three pieces of evidence suggested that there was little difference in the survival rates between male and female tawny owls in Kielder. First, survival rates to first-breeding showed no significant difference between sexes (section 6.3.3). This assumes that the sex ratio of fledged chicks was similar. This was not unreasonable but could not be confirmed as chicks could not be sexed in the nest. Second, in 1990 and 1991 76% of the breeding adults could be aged and, although the mean age of females was slightly higher than males, the difference was not significant (section 6.3.7). Third, the recapture of breeding adults showed no significant difference in the survival rates in males and females (section 6.3.6). In all of these analyses males had consistently lower survival than females although none of the differences were statistically significant. Perhaps with a larger sample, survival may have emerged as significantly different between the sexes. In some other raptors, with a greater degree of size-dimorphism between the sexes, females have significantly higher survival rates

than males (Newton *et al.* 1983a for sparrowhawk *Accipiter nisus*; Picozzi 1984 for hen harrier *Circus cyaneus*).

Another interesting aspect was that the survival of territorial females appeared to have increased by just under 1% per annum during the course of the study (Figure 6.8). Not enough data were available to look at temporal trends in territorial male survival. In contrast survival rates of females to first breeding appear to have changed little, although they may have peaked during the middle years of the study (Figure 6.5). Obviously there was much scatter when these annual survival rates were plotted against time, due largely to the effects of vole abundance on survival rates, so neither of these relationships were significant. The apparent improvement in adult female survival may well reflect the gradual improvement of habitat in the study area for tawny owls (Chapter 4). Between 1980 and 1990 much clear-felling was done, resulting in the gradual creation of a patchwork of different growth stages, with far more hunting opportunities for tawny owls (Petty 1989). The breeding density of owls also increased during this period with vacant territories available each year (Chapter 4). The lack of any relationship between weather in winter (November-February) and survival rates either to first breeding or in territorial females was unexpected. However, there was no really severe winter during this study. In fact winters appear to have become milder, with both the days with air frosts and the days with snow lying decreasing (Chapter 2, Figure 2.9).

Better survival occurred despite an increase in potential predators during the study. The only predators capable of killing free-flying tawny owls in Kielder were goshawks *Accipiter gentilis* which have colonised the area and increased during the study. Tawny owls were recorded as goshawk prey (Petty, unpublished data) but the survival data suggest that goshawk predation had little effect on turnover rates in owls.

Overall annual survival rates in tawny owls of 84-86% were high compared to other studies. Southern (1970) used life tables to compare age-specific mortality rates of tawny owls in his study at Wytham Wood with BTO data from the whole of Britain, as well as with data from Scandinavia (Olssen 1958) and Switzerland (Schifferli 1957). The overall annual survival rates calculated for four age groups (1-2, 2-3, 3-4, 4-5 year old) were 81.5% in Wytham (very small sample size), 56.8% in Britain as a whole, 58.3% in Scandinavia and 65.1% in Switzerland. These survival rates were based on national ringing schemes which often under-estimate survival in raptors (Newton 1979).

Percival (1990) used a method which allowed both age- and time-specific survival rates to be calculated and estimated adult survival at 79% in Scotland/northern England and southeast England, but slightly lower (72%) in southwest England/Wales. The differences between these data and mine could have been due to the analytical methods used, rather than to genuine differences in survival. The only published data on tawny owls which allow survival rates to be calculated using the same method I used, was the study of Delmee *et al.* (1978) in broadleaved woodland in Belgium. Overall annual survival rate of females from 10 territories from 1960 to 1974 was 93.6% (calculated from Table 2).

High proportions of breeding males and females were caught in Kielder in 1990 and 1991, and of these 76% could be accurately aged (Figure 6.9). Around three-quarters (74% in 1990 and 76% in 1991) were reared in years when vole populations were increasing (1984, 1987 and 1990), emphasising both the importance of these cohorts to future generations and the role played by food-supply.

6.5 Summary

1. The analysis of population turnover in Kielder was based on 825 chicks which had been ringed in this study area and 130 females and 63 males caught as breeding adults. Females were caught while breeding during 1980-91 but males were only caught during 1988-91.

2. There was no difference in the natal dispersal direction of males (n=50) and females (n=52). Most birds dispersed in a NW or SE direction, corresponding to the alignment of the main valley system.

3. The geometric mean natal dispersal distance was 2.85 km, with no significant difference between the sexes for movements within the study area. Distribution of natal dispersal distances was positively skewed, suggesting that relatively few birds would have dispersed beyond 10 km. Thirty percent of recorded tawny owls settled to breed within two territories of the natal territory, but none bred in the natal territory itself.

4. Natal dispersal distances were shortest for cohorts reared in years when vole populations were increasing and furthest for cohorts reared in years when vole populations were low, although these differences were not significant.

5. Natal dispersal of females beyond the study area was investigated by trapping in valleys adjacent to the main study areas. There was virtually no movement of females between valleys. However, there was some dispersal between the Kielder study area and another area lower down the same valley system. The natal dispersal distances of such birds ranged between 13.7 km and 26.6 km.

6. From 825 chicks reared (and ringed) in the study area (1979-90), 101 (12.2%) had been recruited into the breeding population by

1991. Recruitment of males (6.1% or 7.3% when corrected) was not significantly different to females (7.1%).

7. Recruitment was significantly related to the phase of the vole cycle when the chicks were born. Cohorts reared in low or increasing vole years, when voles were abundant through the following winter, had the highest recruitment rates of 22% and 19% respectively. Because many chicks were reared in increasing vole years these formed a high proportion of the future breeding population. In contrast, only 4% of chicks reared in declining vole years, when vole populations were at their lowest through the following winter, were recruited into the future breeding population.

8. Birthdate within cohorts reared in different vole year classes also influenced recruitment rate. In years when vole populations were increasing, birthdate appeared to have little effect on the chance of future recruitment. However, in years when vole populations were low or declining, none of the late-hatched chicks were recruited.

9. Most (61%) new females recruited into the breeding population were reared in the study area. The remainder (39%) were unringed and assumed to be immigrants.

10. Recruitment did not appear to have been influenced greatly by the availability of vacant territories, because in every year of the study some territories were unoccupied while other apparently suitable areas had never been occupied.

11. Ninety-seven percent of tawny owls bred for the first time before they were four years old and both sexes were capable of breeding successfully as yearlings. The mean age of first breeding was not significantly different between the sexes, although males recruited slightly earlier.

12. Tawny owls showed a high degree of fidelity to their territories. A change of one or both of the adults largely resulted from the death of the previous occupant/s and its/their replacement with a bird/s breeding for the first time. It was not unusual for territories to be temporarily unoccupied. Single-bird territories were more quickly re-occupied by a pair compared to unoccupied territories.

13. There was very little movement of tawny owls between territories. In 133 territory years (or 266 bird years) only one female and three males (involving four moves) changed to adjacent territories.

14. The mean annual survival rate of territorial females was 85%. Survival rates were highest (91%) between years passing from an increasing to decreasing vole population and lowest (78%) between years passing from a declining to a low vole population. The survival rate of territorial females appears to have increased between 1980 and 1991 by an average of around 0.9% per annum.

15. The mean annual survival rate of territorial males could only be calculated over three pairs of years and was 84%. Over the same period mean annual survival of females was 88%, and not significantly different.

CHAPTER 7

MOULT

7.1 Introduction

7.2 Study area and methods

7.3 Results

7.3.1 Timing of moult

7.3.2 Is moult symmetrical in both wings?

7.3.3 Number of flight feathers moulted annually

7.3.4 What influences the number of flight feathers moulted?

7.3.5 Replacement of juvenile flight feathers.

7.3.6 Sequence of wing feather moult

7.4 Discussion

7.4.1 Moult of wing feathers

7.4.2 Moult of tail feathers

7.4.3 Moult of body feathers

7.4.4 Age determination

7.5 Summary

7.1 Introduction

The replacement of feathers is necessary for both efficient insulation and flight (for reviews see Payne 1972; King 1980). Most passerines undergo a complete annual moult whereas many larger, longer-lived birds replace body feathers annually but may defer the replacement of flight feathers for two or more years. Because additional energy and protein are required for feather growth, most temperate species moult either before or just after breeding, or during a lull in the breeding cycle when energy demands are reduced. Moult is completed before weather conditions deteriorate in the autumn.

The tawny owl *Strix aluco* is a sedentary, nocturnal predator of small mammals (Southern 1970; Mikkola 1983; Cramp 1985). Its moult is complex and has been described in some detail by Piechocki (1961; 1968), Stresemann and Stresemann (1966), Glutz and Bauer (1980), Hardy *et al.* (1981a), Ginn and Melville (1983), Hirons *et al.* (1984) and Cramp (1985). There are considerable differences between some of these accounts.

Successful age determination of individuals depends on a full understanding of moult sequences and the separation of juvenile and adult plumages. Age determination techniques based on moult have been presented for the tawny owl by Baker (1981), Cramp (1985) and Ahola and Niiranen (1986). Only the latter authors successfully illustrate the differences between adult and juvenile remiges, which they use to describe three age classes.

In this chapter I present data from individually known tawny owls which were caught during each nesting attempt when their remiges (primary and secondary feathers) and rectrices (tail feathers) (Figure 7.1) were dye-marked at each capture to check the progression of moult. There were significant annual differences in numbers of wing and tail feathers moulted, depending on reproductive success. I then present a set of criteria based on the

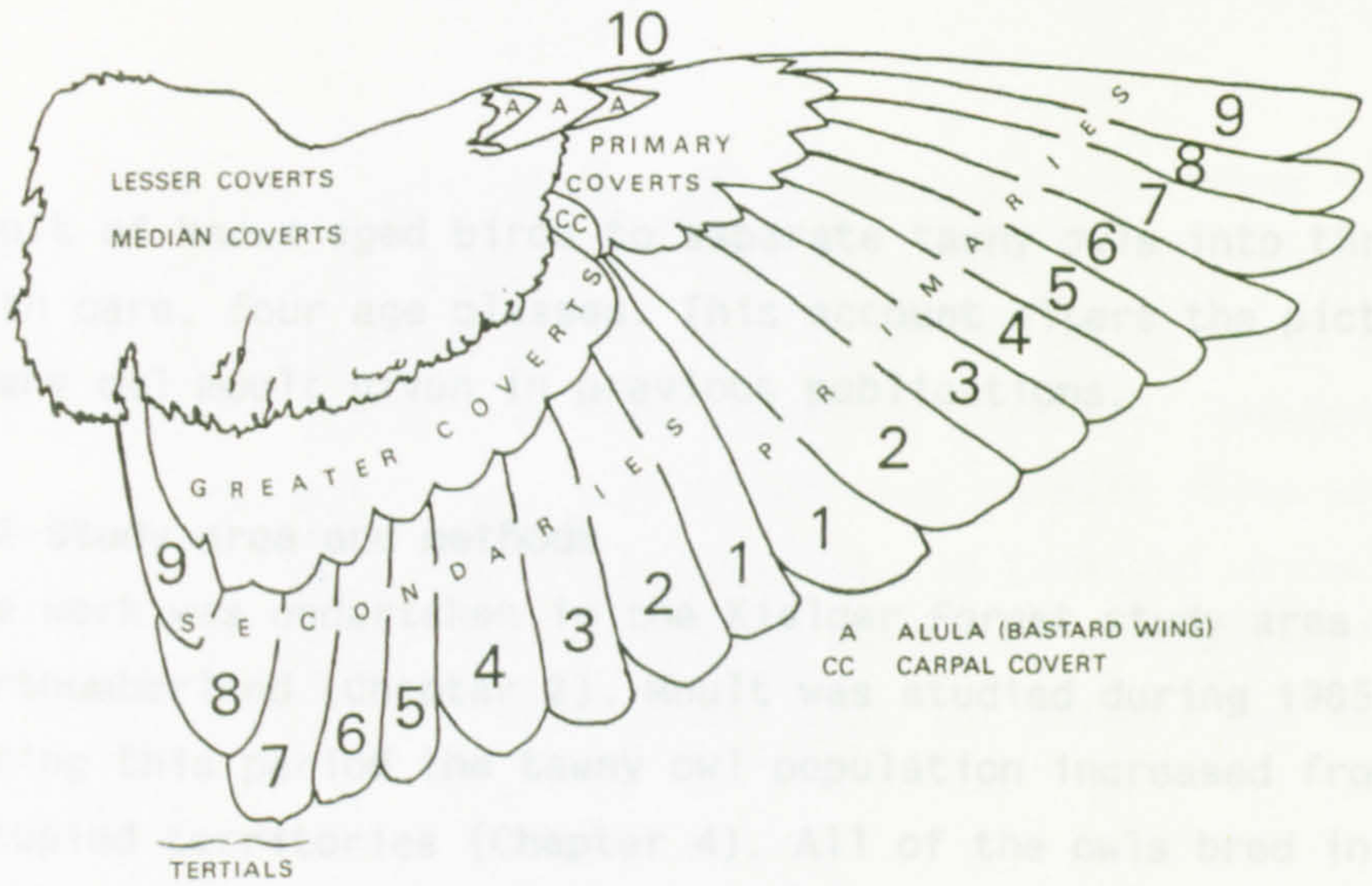


Figure 7.1 Drawing of a birds wing showing the numbering of primary and secondary feathers and the position of other feather groups referred to in the text (redrawn from Ginn and Melville 1983).

Plate 7.1 Moult in tawny owls was investigated by dying with picric acid the flight feathers of breeding adults prior to their annual moult, and then recapturing them a year latter. This is typical of a bird that had successfully reared chicks, replacing only S1, S10 and S11 (not dyed) after breeding. Non-breeding birds and those failing in a breeding attempt moult considerably more feathers (see text).

moult of known-aged birds to separate tawny owls into three, and with care, four age classes. This account alters the picture of tawny owl moult given in previous publications.

7.2 Study area and methods

The work was undertaken in the Kielder Forest study area in Northumberland (Chapter 2). Moult was studied during 1985-1991. During this period the tawny owl population increased from 50 to 66 occupied territories (Chapter 4). All of the owls bred in nestboxes (Petty 1987b). Female owls were caught at the nestbox with a hand-held net similar in shape to a butterfly net, and male owls were caught in a trap which was placed over the entrance to the nestbox (Chapter 6). Most breeding females were caught each time they bred during 1985-1991 and males during 1988-1991. Adult owls were usually caught when the oldest chick was 5-15 days old.

The presence of active flight feather moult (growing feathers) was checked in each owl caught during the incubation and nestling periods. Tawny owls have 10 primary and 13 secondary feathers in each wing and 12 tail feathers. Feathers were numbered, from 1-13 inwards towards the body for secondaries (feathers 11-13 are sometimes classed as tertials), from 1-10 outwards from the body for primaries, and from 1 (central feather) to 6 (outer feather) for the left and right-hand sides of the tail. The first time a bird was caught, part of the white area on the underside of these 58 feathers was dyed yellow with picric acid in a solution of 70% alcohol plus a wetting agent. During subsequent recaptures the positions of any new feathers (undyed) were recorded and the new feathers were dyed (Plate 7.1). Feathers stained with picric acid did not fade through time as the staining was a result of a chemical reaction with keratin, so re-dying was not necessary. The moult of primary and secondary feathers was termed symmetrical if feathers were replaced in the same sequence in both wings each year; if not, the moult was termed asymmetrical.

Owls were not always caught every year, but providing they were caught every second year, feathers moulted in the first or second year could be identified by looking at the white basal area on the underside of the primary and secondary feathers. Feathers replaced on the last moult had a pink/brown wash to this white area while those replaced on the previous moult had faded to white. It was not possible to do the same with tail feathers, so the sample sizes for tail moult analysis were smaller than for primary and secondary feathers.

The analyses treat each annual moult record from an owl independently, although moult data from the same individual, but in different years were used.

Four age categories were used, namely:
One-year-old. From birth until prior to the first adult moult in the second year of life.
Two-year-old. From the end of the first adult moult until the start of the second moult in the third year of life.
Three-year-old. From the end of the second adult moult until the start of the third moult in the fourth year of life.
Three-plus-year-old. From the end of the third adult moult in the fourth year of life.

Brood size in tawny owls was the number of chicks fledging (leaving the nest site). Pairs of owls which failed to rear chicks could be classed either as those which laid and then failed during the incubation or the nesting period, or those which failed to lay altogether.

The main food of the tawny owl in the study area was the field vole *Microtus agrestis*. The population of these rodents exhibited a pronounced three-year cycle of abundance (Chapter 3). Years could be classified according to vole populations as low (1986, 1989) increasing (1987, 1990) or decreasing (1985, 1988). In low vole

years few pairs of tawny owls even laid, and those that did produced small broods. In both increasing and decreasing vole years a high proportion of tawny owls bred and successfully reared chicks (Chapter 5).

7.3 Results

7.3.1 Timing of moult

In 226 owls that were recaptured during the nestling period, none out of 62 males were moulting wing or tail feathers. In 164 females, one bird had six primaries in growth, one had two secondaries in growth and five had one secondary in growth. None had active tail moult. Moult of flight feathers mainly commenced in both sexes once the chicks had left the nest in May-June. Evidence came from the presence of moulted flight feathers in the territory. Therefore, most birds caught during a breeding attempt had not started their annual moult. Moult usually ceased before the end of September (Hardy *et al.* 1981a; Hirons *et al.* 1984). There was some evidence that non-breeding birds moult earlier than breeders (Hirons *et al.* 1984; Petty unpublished data).

7.3.2 Is moult symmetrical in both wings?

The moult of primary and secondary feathers was more often than not asymmetrical, that is feathers were not replaced in the same sequence in both wings (Table 7.1). Only with primary feathers in males did the number of birds with asymmetrical versus symmetrical moult show no significant difference.

7.3.3 Number of flight feathers moulted annually

There was considerable variation in the number of flight feathers moulted annually (Table 7.2). A surprising number (17-19%) of owls replaced no primary feathers in a particular year, while very few (1-6%) replaced all 20. Males appeared to moult slightly more primary feathers at each moult than females (Table 7.2), but there was no significant difference between the sexes in the median

Table 7.1 The number (%) of tawny owls with symmetrical or asymmetrical moult between wings, based on the feather replacement at the last moult.

Moult pattern	Females		Males	
	Primaries	Secondaries	Primaries	Secondaries
Symmetrical	78 (37.1)	47 (22.0)	39 (42.9)	12 (13.2)
Asymmetrical	132 (62.9)	167 (78.0)	52 (57.1)	79 (86.8)
Overall	210(100.0)	214(100.0)	91(100.0)	91(100.0)
Chi-squared	13.89,p<0.001	67.29,p<0.001	1.86,p>0.5	49.33,p<0.001

The expected values for the chi-squared test were based on an equal number of birds having symmetrical and asymmetrical moult.

Table 7.2 The number (%) of flight feathers moulted annually by tawny owls in Kielder (1985-1990). Each owl has 12 tail feathers, 20 primary and 26 secondary feathers (both wings).

Number of feathers moulted	Primaries		Secondaries		Tail	
	female	male	female	male	female	male
0	40 (18.7)	15 (16.5)	3 (1.4)	0 (0.0)	38 (23.3)	22 (30.1)
1	25 (11.7)	6 (6.6)	1 (0.5)	0 (0.0)	15 (9.2)	6 (8.2)
2	13 (6.1)	7 (7.7)	7 (3.3)	4 (4.4)	6 (3.7)	8 (11.0)
3	18 (8.4)	2 (2.2)	7 (3.3)	3 (3.3)	14 (8.6)	5 (6.9)
4	12 (5.6)	9 (9.9)	11 (5.1)	5 (5.5)	11 (6.8)	1 (1.4)
5	10 (4.7)	4 (4.4)	12 (5.6)	8 (8.8)	3 (1.8)	1 (1.4)
6	8 (3.7)	6 (6.6)	14 (6.5)	7 (7.7)	2 (1.2)	0 (0.0)
7	8 (3.7)	3 (3.3)	23 (10.7)	5 (5.5)	4 (2.5)	2 (2.7)
8	6 (2.8)	4 (4.4)	14 (6.5)	8 (8.8)	8 (4.9)	1 (1.4)
9	6 (2.8)	5 (5.5)	19 (8.9)	2 (2.2)	10 (6.1)	3 (4.1)
10	12 (5.6)	5 (5.5)	13 (6.1)	4 (4.4)	9 (5.5)	6 (8.2)
11	7 (3.3)	3 (3.3)	10 (4.7)	4 (4.4)	13 (8.0)	3 (4.1)
12	8 (3.7)	1 (1.1)	10 (4.7)	5 (5.5)	30 (18.4)	15 (20.6)
13	3 (1.4)	3 (3.3)	5 (2.3)	3 (3.3)		
14	7 (3.3)	3 (3.3)	12 (5.6)	4 (4.4)		
15	5 (2.3)	0 (0.0)	10 (4.7)	4 (4.4)		
16	9 (4.2)	4 (4.4)	6 (2.8)	4 (4.4)		
17	5 (2.3)	3 (3.3)	10 (4.7)	4 (4.4)		
18	5 (2.3)	3 (3.3)	11 (5.1)	2 (2.2)		
19	4 (1.9)	0 (0.0)	5 (2.3)	4 (4.4)		
20	3 (1.4)	5 (5.5)	7 (3.2)	1 (1.1)		
21			4 (1.9)	6 (6.6)		
22			0 (0.0)	1 (1.1)		
23			0 (0.0)	1 (1.1)		
24			0 (0.0)	1 (1.1)		
25			0 (0.0)	1 (1.1)		
26			0 (0.0)	0 (0.0)		
Number of owls	214 (100)	91 (100)	214 (100)	91 (100)	163 (100)	73 (100)
Median number of feathers moulted	4	6	9	10	4	3

number of feathers moulted annually (Mann-Whitney U-test, Z=-1.179, P>0.05).

In contrast to the moult of primary feathers, very few owls failed to moult some secondary feathers, but none moulted all 26 (Table 7.2). Again males appeared to moult slightly more secondaries than females, but with no significant difference between the sexes in the median numbers of feathers moulted (Z=-0.903, P>0.05).

The pattern of tail feather moult was quite different to that of wing moult. In a given year most owls moulted either none or all 12 tail feathers (Table 7.2). This was because tail feathers were replaced in total every second year in most owls (see later).

7.3.4 What influences the number of flight feathers moulted?

Variation in the annual replacement of wing feathers was related to breeding success. Birds that failed to lay moulted the most primary and secondary feathers, while those rearing the largest broods moulted fewest (Table 7.3). The number of wing feathers moulted by males and females showed a similar significant relationship with breeding success. However, in males the number of chicks reared (1-4) was progressively associated with a decrease in the number of wing feathers moulted, particularly primaries. In females, however, the number of wing feathers moulted showed less variation with brood size (Table 7.3 and Figure 7.2).

Breeding success in tawny owls was related to vole abundance (Chapter 5), so wing feather moult but not tail moult was also related to vole abundance (Table 7.4). There were great similarities between the sexes in the numbers of primary, secondary and tail feathers moulted in each vole year class (low, increasing or decreasing). Males moulted slightly more primary and secondary feathers than females (Table 7.4). In low vole years significantly more primary and secondary feathers were moulted than in the other vole year classes (Figure 7.3). In increasing and decreasing vole

Table 7.3 The mean number of flight feathers moulted annually in tawny owls in relation to sex and brood size, Kielder 1985-90.

Brood size	Primary feathers				Secondary feathers				Tail feathers			
	Mean	n	SE	RT	Mean	n	SE	RT	Mean	n	SE	RT
Female												
NB	13.17	48	0.69	D	15.69	48	0.57	B	6.60	25	1.08	A
0	8.56	16	1.23	C	11.82	16	1.48	AB	7.36	11	1.56	A
1	5.06	17	1.28	ABC	9.18	17	1.18	A	5.77	13	1.49	A
2	5.72	46	0.81	BC	8.33	46	0.63	A	5.63	38	0.80	A
3	2.54	52	0.42	A	7.85	52	0.53	A	5.04	43	0.65	A
4-5	3.40	35	0.67	AB	8.71	35	0.73	A	4.94	33	0.76	A
ANOVA	F=33.24, P<0.001				F=21.86, P<0.001				F=0.77, P>0.05			
Male												
NB	13.67	21	1.00	D	18.00	21	0.90	B	6.18	17	1.34	A
0	10.86	7	2.25	CD	12.43	7	2.74	AB	10.00	4	1.68	A
1	9.38	8	2.19	ACD	11.13	8	1.44	A	5.57	7	1.78	A
2	5.96	23	1.14	ABC	9.09	23	1.13	A	3.44	16	1.00	A
3	3.04	25	0.58	AB	7.84	25	0.80	A	4.04	23	1.03	A
4-5	1.43	7	0.54	A	8.57	7	2.17	A	6.00	6	2.42	A
ANOVA	F=16.40, P<0.001				F=12.05, P<0.001				F=1.60, P>0.05			

Brood size = number of chicks fledging; NB = not breeding; 0 = birds which laid but failed to rear any chicks.

RT = Scheffe range test (95%); similar letter denote no significant difference.

Table 7.4 The mean number of flight feathers moulted annually in tawny owls in relation to sex and vole year classes, Kielder 1985-90.

Vole year class	Primary feathers				Secondary feathers				Tail feathers			
	Mean	n	SE	RT	Mean	n	SE	RT	Mean	n	SE	RT
Female												
1	12.84	58	0.65	A	14.50	58	0.63	A	5.86	35	0.87	A
2	3.95	102	0.43	B	9.77	102	0.46	B	5.24	93	0.47	A
3	4.09	54	0.61	B	6.59	54	0.44	C	6.37	35	0.85	A
ANOVA	F=79.67, P<0.001				F=46.10, P<0.001				F=0.78, P>0.05			
Male												
1	13.37	30	0.88	A	16.40	30	0.97	A	5.30	23	1.06	A
2	4.42	37	0.76	B	10.27	37	0.78	B	4.72	36	0.79	A
3	4.38	24	0.83	B	6.13	24	0.77	C	5.43	14	1.54	A
ANOVA	F=40.39, P<0.001				F=32.99, P<0.001				F=0.14, P<0.05			

Vole year class: 1 = low, 2 = increasing, 3 = declining

RT = Sceffe range test (95%), similar letter denote no significant difference.

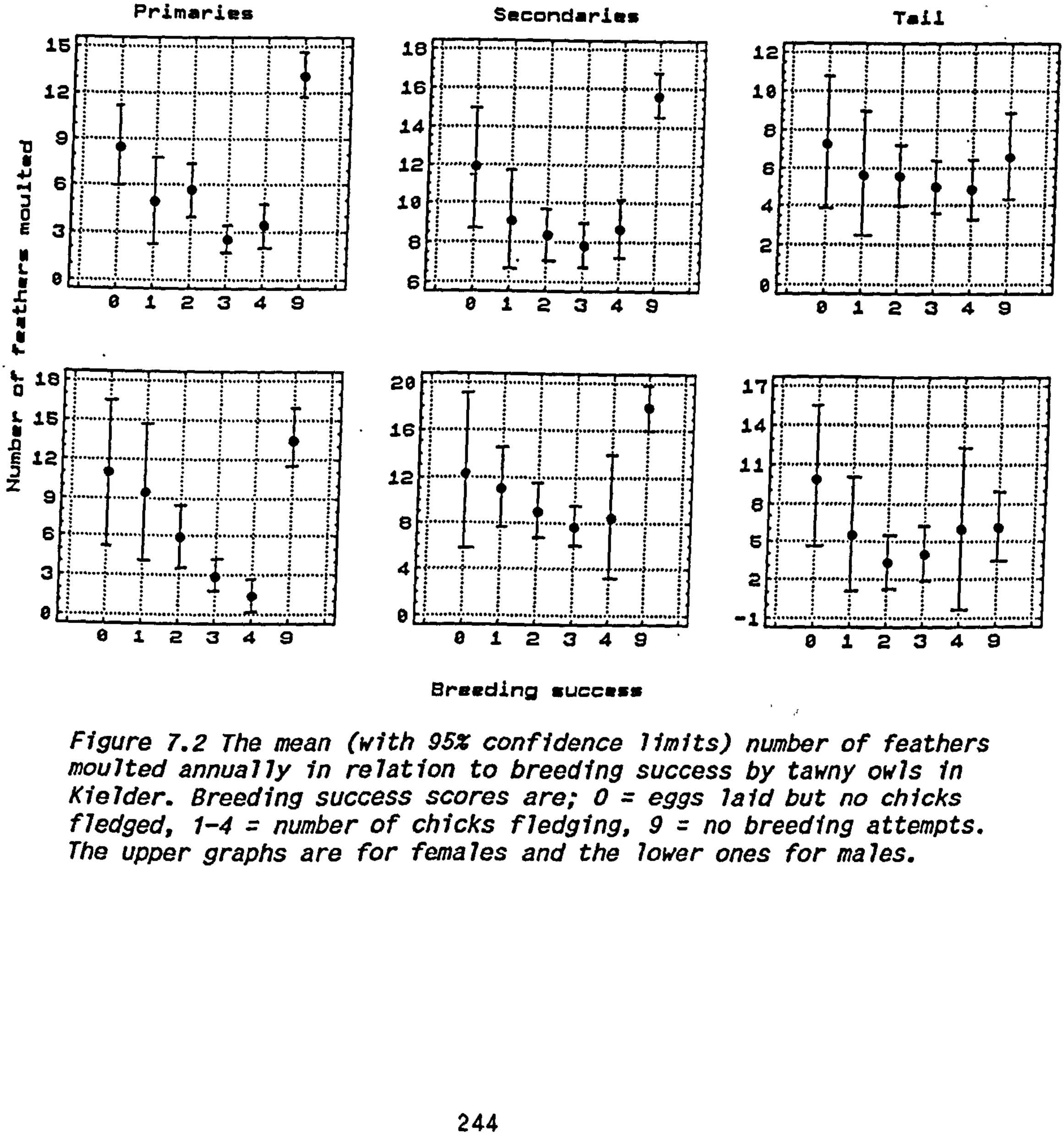


Figure 7.2 The mean (with 95% confidence limits) number of feathers moulted annually in relation to breeding success by tawny owls in Kielder. Breeding success scores are; 0 = eggs laid but no chicks fledged, 1-4 = number of chicks fledging, 9 = no breeding attempts. The upper graphs are for females and the lower ones for males.

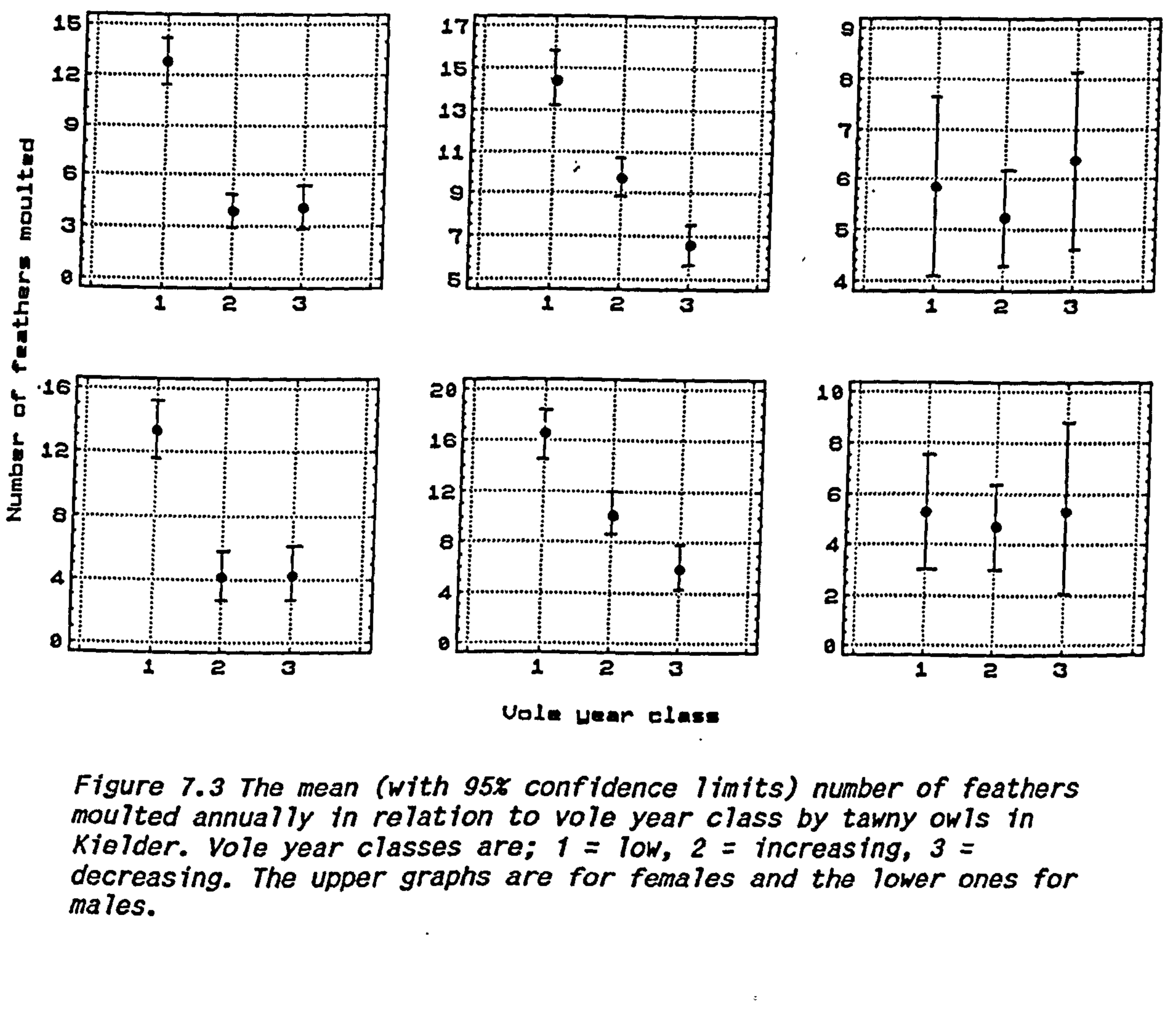


Figure 7.3 The mean (with 95% confidence limits) number of feathers moulted annually in relation to vole year class by tawny owls in Kielder. Vole year classes are; 1 = low, 2 = increasing, 3 = decreasing. The upper graphs are for females and the lower ones for males.

years there were no significant differences in the numbers of primary feathers moulted (Table 7.4), but significantly fewer secondaries were moulted in decreasing than in increasing vole years.

The number of primary feathers moulted in a given year was positively related to the number of secondary feathers moulted (males $r=0.72$, $df=90$, $P<0.001$; females $r=0.64$, $df=213$, $P<0.001$). Hence, moulting more primaries did not lead to a decrease in the number of secondaries moulted.

In contrast, there was no relationship between the number of tail feathers moulted and breeding success (Table 7.3), vole year type (Table 7.4) or total wing feathers moulted (males $r=0.14$, $df=72$, $P>0.05$; females $r=0.01$, $df=162$, $P=>0.05$). Nor could I find any other factor related to tail feather moult.

7.3.5 Replacement of juvenile flight feathers.

Except for flight feathers (primary, secondary and tail feathers) and primary coverts (Figure 7.1), tawny owls replace all feathers grown during the nestling stage in late summer/early autumn of their first year. There are distinct differences in pattern, shape and colour between juvenile and adult flight feathers. Juvenile tail feathers have a white tip which is pointed. Adult tail feathers are more rounded, with an off-white tip with many brown flecks (Plate 7.2). Juvenile wing feathers have a broken or thin dark terminal band (Plate 7.3). In contrast, adult wing feathers usually have a broad, unbroken terminal band and may have a different colour and/or pattern to juvenile feathers (Plate 7.4). Juvenile flight feathers are progressively replaced by adult feathers starting at the first flight feather moult in the second year of life. I investigated this aspect with tawny owls of known age (ringed as nestlings).

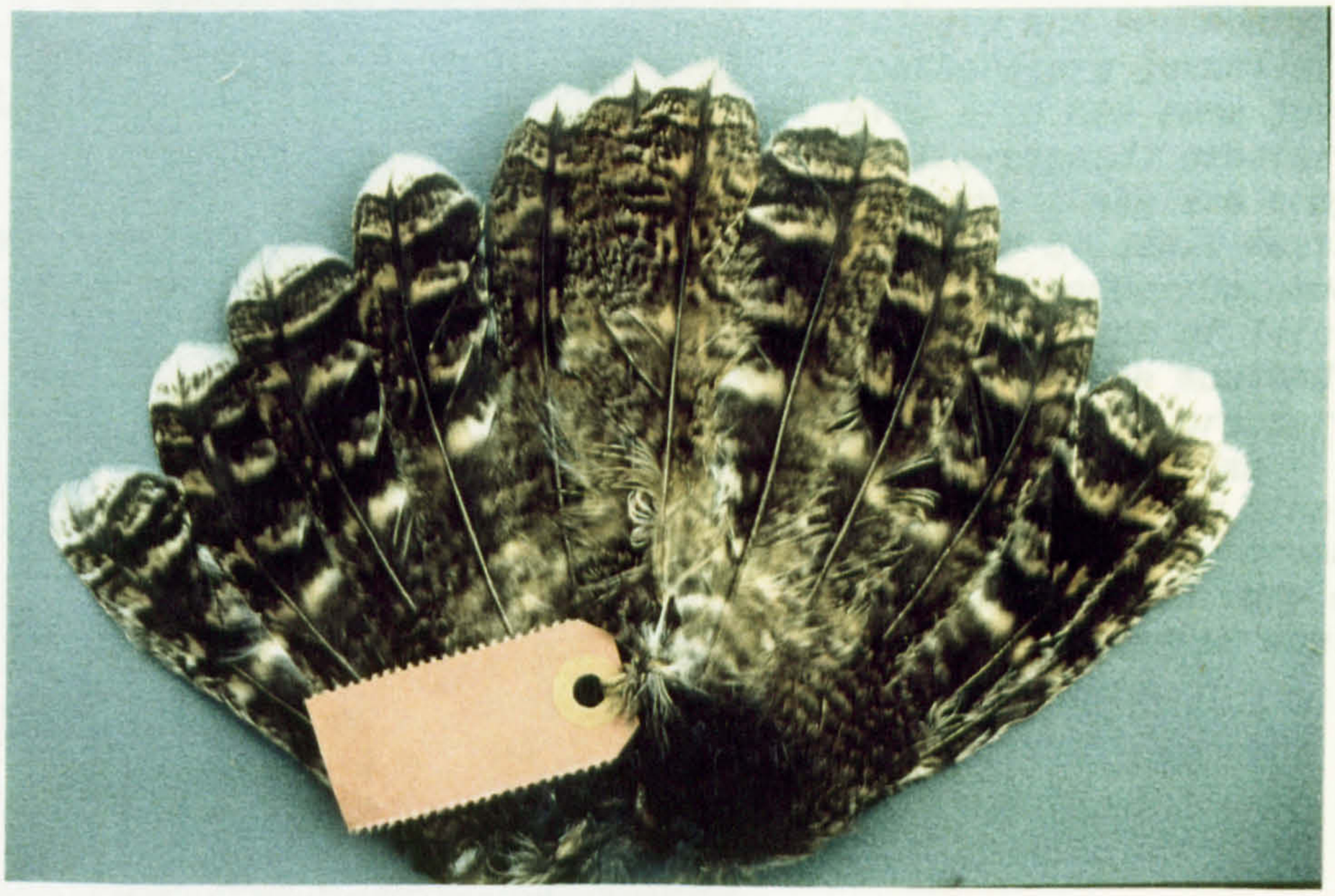


Plate 7.2 Typical juvenile (upper) and adult tail (lower) of tawny owl.

Plate 7.3 One-year-old, prior to its first moult in its second year of life. All the primary and secondary feathers are juvenile. This bird also has some juvenile (white-tipped) greater coverts, these are completely replaced by adult feathers before November/December in the first year of life. Some birds may have moulted all their juvenile greater coverts as early as September/October. The retained juvenile primary coverts are also very evident against the darker adult alula feathers.

Plate 7.4 Two-year-old, prior to its second moult in its third year of life. During the first moult only two primary feathers (P5 and P6) were replaced by adult feathers, the rest are juvenile feathers. Primary moult usually commences with P5 and P6 and then progresses both outwards to P10 and inwards to P1. None of the outer secondary feathers were moulted, S1 - S10 are juvenile.

Plate 7.5 Three-year-old, prior to its third moult in its fourth year of life. All the primary feathers have now been replaced by adult feathers. Juvenile secondary feathers are still retained at S1, S4, S7, S8 and S11. Many three-year-old birds retain at least one juvenile feather, S4 or occasionally S1 and/or S7 are usually the last to be replaced. Retained juvenile feathers are usually very well worn in three-year-old birds and need to be distinguished from old and worn adult feathers. It is sometimes difficult to distinguish between two-year and three-year-old birds. With these it is necessary to determine whether one (two-year-old) or two (three-year-old) generations of adult feathers are present. To do this, turn the wing over and look at the white area at the base of the primary and secondary feathers. It is best to blow or move the underwing coverts to one side. Feathers that were replaced on the last moult have a pink/brown (brown feathers) wash to this white area, while feathers replaced on the last but one moult do not (white feathers). Therefore, birds with a mixture of white and brown feathers are three-year-olds, while two-year-olds have brown feathers only. In poor light and sunny conditions it may not be possible to detect these two types of adult feathers. Overcast but reasonably bright conditions are the best.

All twelve juvenile tail feathers were replaced at the first adult moult. All yearlings (31 females and 30 males) caught prior to their first adult moult had complete juvenile tails. In contrast, all two-year olds (13 females and 18 males) before their second adult moult had complete adult tails. All three- and four-year old owls had complete adult tails too.

In contrast, many juvenile wing feathers were retained beyond the first adult moult and some beyond the second and even third adult moult. This held for both sexes, but males appeared to replace juvenile feathers sooner than females (Tables 7.5 and 7.6).

Table 7.5 Number of juvenile primary feathers present in tawny owls by age and sex, Kielder 1985-1990.

Number of juvenile feathers	Age *							
	1		2		3		4	
	female	male	female	male	female	male	female	male
0	-	-	-	-	23(88.5)	13(81.3)	23(100.0)	9(100.0)
1	-	-	-	-	1 (3.8)	1 (6.3)	-	-
2	-	-	-	-	2 (7.7)	1 (6.3)	-	-
3	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-
5	-	-	-	1 (5.0)	-	-	-	-
6	-	-	1 (3.6)	1 (5.0)	-	-	-	-
7	-	-	1 (3.6)	-	-	1 (6.3)	-	-
8	-	-	1 (3.6)	-	-	-	-	-
9	-	-	2 (7.1)	-	-	-	-	-
10	-	-	2 (7.1)	1 (5.0)	-	-	-	-
11	-	-	1 (3.6)	5(25.0)	-	-	-	-
12	-	-	-	1 (5.0)	-	-	-	-
13	-	-	-	1 (5.0)	-	-	-	-
14	-	-	5(17.9)	3(15.0)	-	-	-	-
15	-	-	1 (3.6)	1 (5.0)	-	-	-	-
16	-	-	5(17.9)	1 (5.0)	-	-	-	-
17	-	-	2 (7.1)	2(10.0)	-	-	-	-
18	-	-	1 (3.6)	1 (5.0)	-	-	-	-
19	-	-	-	-	-	-	-	-
20	31(100.0)	30(100.0)	6(21.4)	2(10.0)	-	-	-	-
Total birds	31	30	28	20	26	16	23	9
Median number ofjuvenile feathers	20	20	15.5	11.0	0	0	0	0

** Age categories: 1= prior to first adult moult in second year of life, 2 = after first moult and prior to second moult in third year of life, etc.*

Table 7.6 Number of juvenile secondary feathers present in tawny owls by age and sex, Kielder 1985-1990.

Number of juvenile feathers	Age *							
	1		2		3		4	
	female	male	female	male	female	male	female	male
0	-	-	-	-	6(23.1)	6(37.5)	20(87.0)	9(100.0)
1	-	-	-	-	1 (3.8)	4(25.0)	2 (8.7)	-
2	-	-	-	-	7(26.9)	1 (6.3)	-	-
3	-	-	-	-	2 (7.7)	1 (6.3)	1 (4.3)	-
4	-	-	-	-	5(19.2)	1 (6.3)	-	-
5	-	-	-	-	-	-	-	-
6	-	-	-	-	1 (3.8)	-	-	-
7	-	-	-	-	1 (3.8)	1 (6.3)	-	-
8	-	-	-	-	2 (7.7)	1 (6.3)	-	-
9	-	-	-	-	-	-	-	-
10	-	-	-	-	-	-	-	-
11	-	-	-	-	-	-	-	-
12	-	-	-	-	-	1 (6.3)	-	-
13	-	-	-	-	-	-	-	-
14	-	-	2 (7.1)	3(15.0)	1 (3.8)	-	-	-
15	-	-	-	-	-	-	-	-
16	-	-	-	2(10.0)	-	-	-	-
17	-	-	-	1 (5.0)	-	-	-	-
18	-	-	8(28.6)	3(15.0)	-	-	-	-
19	-	-	-	1 (5.0)	-	-	-	-
20	-	-	6(21.4)	4(20.0)	-	-	-	-
21	-	-	2 (7.1)	2(10.0)	-	-	-	-
22	-	-	5(17.9)	-	-	-	-	-
23	-	-	-	-	-	-	-	-
24	-	-	3(10.7)	4(20.0)	-	-	-	-
25	-	-	2 (7.1)	-	-	-	-	-
26	31(100.0)	30(100.0)	-	-	-	-	-	-
Total birds	31	30	28	20	26	16	23	9
Median number ofjuvenile feathers	26	26	20.0	19.5	2-0	1-0	0	0

** Age - see Table 7.5*

All the primary and secondary feathers of yearling owls caught prior to their first adult moult were juvenile (Plate 7.3).

Two-year-olds caught before their second moult had all retained some juvenile feathers through their first moult (Plate 7.4). On this first moult some birds (20% of females and 10% of males) had replaced no primaries, but all birds had moulted some secondaries (Tables 7.5 and 7.6). The median number of retained juvenile

primary feathers was 15.5 and 11.0 (out of 20) for males and females respectively, and for secondaries 20.0 and 19.5 (out of 26).

Of three-year-olds caught before their third moult, 77% of females and 62% of males retained at least one juvenile secondary (Plate 7.5). Fewer birds retained juvenile primary feathers (11% of females and 19% of males).

No four-year-old males or females had retained juvenile primary feathers, but a few (13%) four-year-old females had juvenile secondary feathers (Table 7.6).

Table 7.7 Moult of two female tawny owls (ring numbers GJ73197 and GH40939) through their first five and six annual moult cycles. Both owls were ringed as nestlings.

Bird number	Age*	Wing	Primaries										Secondaries													Tail					
			1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	11	12	13	1	2	3	4	5	6
1	1	L	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J
1	1	R	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J
1	2	L	J	J	J	J	N	N	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	N	N	N	N	N	N	N
1	2	R	J	J	J	J	N	N	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	N	N	N	N	N	N	N
1	3	L	J	N	N	N	O	O	N	N	N	N	J	N	N	J	N	N	N	N	N	O	O	O	N	O	O	O	O	O	O
1	3	R	J	N	N	N	O	O	N	N	N	N	J	N	N	J	N	N	N	N	N	O	O	N	N	N	O	N	N	O	O
1	4	L	N	O	O	O	N	N	O	O	O	O	N	O	O	N	O	O	O	O	O	N	N	N	N	N	N	N	N	N	N
1	4	R	N	O	O	O	O	N	O	O	O	O	N	O	O	N	O	O	O	O	O	N	N	O	O	O	N	O	O	N	N
1	5	L	O	O	O	O	O	O	N	N	N	N	O	O	O	O	N	O	N	N	N	O	O	O	N	O	O	O	O	O	O
1	5	R	O	O	O	O	N	O	N	N	N	N	O	O	O	O	N	O	N	N	N	O	O	N	N	N	X	O	N	N	O
1	6	L	O	N	N	N	O	N	O	O	O	O	O	N	N	O	O	N	O	O	O	N	N	N	N	N	N	N	N	N	N
1	6	R	O	N	N	N	O	N	O	O	O	O	O	N	N	O	O	N	O	O	O	N	N	O	N	N	N	O	O	N	N
2	1	L	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J
2	1	R	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J	J
2	2	L	J	J	J	J	N	N	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	J	J	J	N	N	N	N	N
2	2	R	J	J	J	J	N	N	J	J	J	J	J	J	J	J	J	J	J	J	J	N	N	N	J	J	N	N	N	N	N
2	3	L	N	N	N	N	O	O	N	N	J	J	J	N	N	J	N	N	N	N	O	O	N	N	N	O	O	O	O	O	O
2	3	R	N	N	N	N	O	O	N	N	J	J	J	N	N	J	N	N	N	N	O	O	O	N	N	O	O	O	O	O	O
2	4	L	O	O	O	O	O	O	O	O	N	N	N	O	O	N	O	O	O	O	O	N	O	N	N	N	N	N	N	N	N
2	4	R	O	O	O	O	O	O	O	O	N	N	N	O	O	N	O	O	O	O	O	N	O	O	N	N	N	N	N	N	N
2	5	L	O	O	O	O	N	O	O	O	O	O	O	O	O	O	N	O	O	O	N	O	O	O	O	O	O	O	O	O	O
2	5	R	O	O	O	O	N	O	O	O	O	N	O	O	O	O	N	O	O	O	N	O	O	O	O	O	O	O	O	O	O
2	6	L	N	N	N	N	O	N	N	N	N	N	O	N	N	O	O	N	N	N	O	N	N	N	N	N	N	N	N	N	N
2	6	R	N	N	N	N	O	N	N	N	O	O	O	N	N	O	O	N	N	N	O	N	N	N	N	N	N	N	N	N	N
2	7	L	O	O	O	O	N	O	O	O	O	O	N	O	O	O	N	O	O	O	N	O	O	N	N	O	O	O	O	O	O
2	7	R	O	O	O	O	N	O	O	O	N	O	N	O	O	O	N	O	O	O	N	O	O	O	N	O	O	O	O	O	O

** Age – see Table 7.5*

J = juvenile feather; N = new adult feather grown during the last moult; O = old adult feather not replaced at the last moult; X = feather missing

7.3.6 Sequence of wing feather moult

Primary and secondary feathers appeared to be replaced in a predetermined sequence (Table 7.7). In the first moult of primary feathers, P5-6 were the first feathers to be shed in most individuals. Moult then progressed both inwards to P1 and outwards to P10. Secondary moult also followed a predetermined sequence with moult first commencing in most birds at S10-11, then S6-7 and S2-3 and progressing both inwards and outwards from these centres. S11-13 (tertials) appeared to be replaced more frequently than other wing feathers. This initial moult sequence appeared to be maintained thereafter, with moult commencing each year where it ceased in the previous year.

7.4 Discussion

7.4.1 Moult of wing feathers

Most previous reports of wing feather moult in tawny owls suggest that all feathers were replaced annually (Piechocki 1968; Hardy *et al.* 1981a; Ginn and Melville 1983; Hirons *et al.* 1984), whereas some studies suggest that wing feather moult was rarely completed (Stresemann and Stresemann 1966; Glutz and Bauer 1980).

My study demonstrated clearly that the number of wing feathers moulted was closely related to breeding success, which in turn was related to food abundance. In my study area tawny owls fed largely on field voles, which had a pronounced three-year cycle of abundance. Most tawny owl pairs bred and reared broods in years when vole populations were increasing or decreasing. In these years relatively few primary and secondary feathers were moulted, probably because of the high energy demands of rearing chicks. There is some evidence that non-breeding birds start to moult earlier than those that breed (Hirons *et al.* 1984; Petty unpublished data).

After leaving the nest, young tawny owls are dependent on their parents for about three months (Southern 1970; Petty and Thirgood

1989). So juveniles do not become independent until mid to late August, and most adult owls have finished moulting by the end of September (Hirons *et al.* 1984).

Moult requires energy and is often associated with a substantial reduction in locomotory activity (Newton 1966). Wijnandts (1984) recorded a reduction from a 100% pre-moult level to 45% at peak moult in late August in long-eared owls *Asio otus*. Ceska (1980) reported a similar depression in locomotion during tawny owl moult. Tawny owls with dependent young cannot afford to reduce locomotory activity, and thus their moult is delayed. Once their offspring have dispersed little time is left for moulting, and it may be essential for their own survival to channel surplus energy into replacing body feathers (see later) rather than wing feathers.

Primary feathers provide forward propulsion while the secondary feathers provide lift. Therefore, a perch hunter like the tawny owl may not be dependent on its wing feathers being in perfect condition, or for moult to be symmetrical in both wings, thus allowing energy to be more appropriately channeled into breeding rather than wing feather replacement. In contrast, sparrowhawks *Accipiter nisus* are more agile aerial hunters which are dependent on the efficiency of their wing feathers, and replace all primary and most secondary feathers annually (Newton and Marquiss 1982b). Unlike tawny owls, female sparrowhawks commence their wing and tail feather moult during incubation at a time when energy requirements are low. This ensures that enough time is available to replace all wing feathers before autumn. Failure to do so may reduce hunting success and jeopardise their own survival through the winter. In sparrowhawks, there was also very little difference between wings in the timing at which feathers were replaced. Newton and Marquiss (1982b) showed from birds in moult that only 1% of females had asymmetrical primary feather moult while 21% had asymmetrical secondary feather moult. In contrast, far more tawny owls replaced

both primary (57% for males, 63% for females) and secondary feathers (87% for males, 78% for females) asymmetrically.

Ginn and Glue (1974) and Hirons *et al.* (1984) recorded differences between wings in the order that tawny owl primary feathers were replaced (asymmetrical moult). They assumed this was unusual and attributed it to birds being in poor condition or diseased. Hirons *et al.* (1984) stated that "in healthy birds the rate at which primaries were replaced was similar in both wings" (symmetrical moult). The present study clearly shows that asymmetrical moult of primary and secondary feathers is normal in tawny owls.

In my study, most tawny owls did not breed every third year when the vole population reached the low point in the cycle. In these years many more primary and secondary feathers were moulted, even though food was scarce. Without the constraints of a family, tawny owls could spread their moult over a substantially longer period, extending from April/May until September/October. However, even in these years most tawny owls did not undergo a complete moult of primary and secondary feathers (Table 7.4).

Most studies of tawny owls have shown them to be dependent on rodents that exhibit pronounced annual population fluctuations (Southern 1970; Delmée *et al.* 1978; this study). Therefore, annual variations in breeding success related to changes in food abundance are likely to have the same influence on moult. Support for this comes from studies in Finland and North America of other closely-related owls in the genus *Strix* (Chapter 1).

Forsman (1981) working with spotted owl *Strix occidentalis* in Oregon was one of the first to record incomplete and asymmetrical annual wing moult in a *Strix* spp. Pietiäinen *et al.* (1984) demonstrated with Ural owl *Strix uralensis* in Finland a very similar moult pattern to that of tawny owls in Kielder. Most wing feathers were moulted when the birds did not breed or failed in a

breeding attempt, and least when three or more chicks were reared. The only disparity between the Pietiäinen *et al.* (1984) study and mine was that Ural owls showed variation in the period that particular primaries and secondaries were kept. For instance, the longest primary feathers (P4-7) in one female were moulted only once in five annual moults. The remaining primaries were renewed two or three times, as were most of the secondaries. The adaptive significance of such a system is unclear. In tawny owls, wing feather moult starts from where it ceased in the previous year (Table 7.7). There was no indication that some feathers were replaced two-three times more frequently than others, although S11-13 (tertials) appear to moult more frequently than other wing feathers (Table 7.7). However, some feathers may be retained longer than others depending on reproductive success. The study of Pietiäinen *et al.* (1984) was based entirely on wild female owls which were caught each time they bred. They distinguished feathers as new (replaced on the last moult) or old by the amount of wear and fading present.

Very few other studies apart from Pietiäinen *et al.* (1984) and mine on wing feather moult in *Strix* owls have been based on recaptures of known, wild individuals. Some previous accounts have relied heavily on captive birds (Piechocki 1968; Forsman 1981). Captive birds are not usually stressed by food shortage and often not by breeding either, so they should be expected to moult far more extensively each year than wild owls. This may account for the differences in some of the published accounts of wing feather moult in tawny owls. The studies of Hardy *et al.* (1981a) and Hirons *et al.* (1984) relied mainly on corpses and data from moult cards from the British Trust for Ornithology. These cards record which wing or tail feathers are growing (in various stages) and those that are not (Ginn and Melville 1983).

Hardy *et al.* (1981a) and Hirons *et al.* (1984) stated that primary feathers were moulted annually in a descendant manner (from the

innermost primary outwards) but provided no evidence for this. So a bird with P5 and P6 in moult would be classed as having moulted P1-4 but not P7-10 (Plate 7.4 as an example), while a bird with P10 in moult would be classed as having moulted P1-9. From the irregular moult described in this chapter, the assumption that P1-5 in the first bird and P1-9 in the second bird were new may be wrong, as may the assumption that P7-10 in the first bird were old feathers.

Clearly, the use of corpses or BTO moult data have limitations for investigating the number of wing feathers shed annually in species with interrupted moult, such as the tawny owl. Hopefully, future studies of moult in owls will concentrate on repeat observations of known individuals in the wild, ideally using some permanent mark on each feather.

There was virtually no overlap in the 95% confidence intervals of numbers of wing feathers moulted in non-breeding and breeding birds (Figure 7.2). Therefore, the numbers of wing feathers moulted can be used retrospectively to determine whether a bird bred or not in the previous year. This is useful in population studies when the breeding success of a bird in the previous year was unknown. With most tawny owls the number of wing feathers replaced on the last moult can be reasonably estimated (apart from S11-13) from wear/fading; dyeing is not essential.

7.4.2 Moult of tail feathers

All accounts of the moult of tail feathers in tawny owls suggest that all twelve feathers are moulted annually and almost simultaneously (Piechocki 1968; Ginn and Melville 1983; Cramp 1985).

My analysis shows that most owls moult their tail feathers biennially. All birds of both sexes completely moulted their tail feathers for the first time at their first adult moult in their second year of life. Thereafter in most birds, feathers were

replaced in alternate years. There were at least two instances where owls retained all tail feathers for an extra year. In other cases one or more feathers were moulted out of sequence with the rest (Table 7.7). For example, a bird moulted 8, 4, 8, and 4 feathers during four successive annual moults. Perhaps the accidental loss of tail feathers resulted in moulting occurring in intervening years. The closely-related spotted owl in North America appears to follow a similar biennial tail moult, but the initial replacement of the juvenile tail occurs at the second adult moult in the third year of life (Forsman 1981; Moen *et al.* 1991).

My analysis also shows that tail moult in the tawny owl is unrelated to the moult of wing feathers, brood size or food supply. The reason why tail feathers appear to have a pre-determined moult time in contrast to wing feathers may be related to the value of these different feather groups for hunting. Tail feathers are used mainly for steering and braking. These aspects may be more crucial to a perch hunter like the tawny owl than the need for propulsion and lift. Once prey is located, largely by sound, a silent precise descent to the origin of the sound on the ground is vital for successful prey capture (Nishimura and Abe 1988).

7.4.3 Moult of body feathers

Although this study did not specifically consider the moult of body feathers, the evidence indicates that body feathers are replaced annually (Witherby *et al.* 1940; Stresemann and Stresemann 1966; Glutz and Bauer 1980; Cramp 1985).

Tawny owls are extremely well feathered, even the legs and toes have a dense cover. This is probably an adaptation to conserve heat during periods of inactivity, particularly during cold weather. Therefore, it is essential that body feathers should be kept in prime condition. The only way to do this is to replace them annually.

In the long-eared owl, approximately 19% of the total plumage weight was lost between the end of one moult in November and the start of the next in May (Wijnandts 1984). This weight reduction was almost entirely from body feathers due to both wear and loss of feathers. In contrast, flight feathers showed virtually no weight loss. There has been no similar study of feather wear in the tawny owl, but it was reasonable to expect a similar process to occur.

7.4.4 Age determination

Ahola and Niiranen (1986) provide good colour illustrations highlighting the difference between juvenile and adult tawny owl wing feathers. They also provide a reliable guide to determine the age of tawny owls from the presence/absence of adult/juvenile feathers. Their guide can be used to age owls as one-, two- or two-plus-year olds. My data suggest that it is possible to extend this to one additional age category, as a high proportion of three-year olds also retain at least one juvenile feather (Tables 7.5 and 7.6). Table 7.8 (summarizing data from Tables 7.5 and 7.6) can be used in conjunction with Plates 7.3-7.5 to identify four age

Table 7.8 Percentage of tawny owls with juvenile feathers (adult feathers) by age, sex and flight feather group.

Age*	Euring age code	Primaries		Secondaries		Tail	
		female	male	female	male	female	male
1	1,3,5	106 (0)	100 (0)	100 (0)	100 (0)	100 (0)	100 (0)
2	5,7	100 (79)	100 (90)	100(100)	100(100)	0(100)	0(100)
3	7,9	11(100)	19(100	77(100)	63(100)	0(100)	0(100)
3+	9,11	0(100)	0(100)	13(100)	0(100)	0(100)	0(100)

** Age - see Table 7.5*

Euring age codes - see Anon (1984b)

classes. The accuracy of the method can also be established from Table 7.8. It should be 100% reliable at ageing one- and two-year olds, between 63-77% reliable for three-year old and 100% reliable for three-plus-year males and 87% for similar-aged females.

7.5 Summary

1. The number of flight feathers (rectrices and remiges) moulted annually was investigated by dying feathers one year and re-examining the recaptured owls in the following year. The recaptures of 214 females and 91 males from Kielder were used in the analyses.

2. Owls were caught mainly during the nestling period, with a few females being caught during incubation. No males had started their moult and only 5% of females were in moult during this period.

3. Flight feather moult in breeding adults commenced once the chicks had fledged. It appeared to start earlier in birds that did not breed or those that failed in a breeding attempt.

4. Asymmetrical moult of wing feathers (primaries and secondaries) was more frequent than symmetrical moult in both sexes.

5. There was considerable variation in the number of flight feathers moulted annually. Males moulted slightly more wing feathers each year than females but the differences were not significant. The median number of primary feathers moulted annually for males and females was 6 and 4 respectively out of a total of 20. For secondary feathers it was 10 and 9 out of 26, and for tail feathers it was 3 and 4 out of 12. Each year moult started from where it ceased in the previous year.

6. Wing feather moult was significantly related to breeding success. Birds that did not breed moulted most feathers, while those that reared the largest broods moulted fewest.

7. Breeding success of tawny owls was significantly related to a three-year cycle of field vole abundance. Therefore, because moult was related to breeding success, it was also indirectly related to vole abundance. The result was that tawny owls moulted most wing feathers in years of low vole abundance, when most did not breed,

and fewest in years of high vole numbers (increasing and decreasing vole year classes) when most pairs bred.

8. Tail feather moult was not related to breeding success, or to any other factor investigated. Most birds replaced all twelve tail feathers biennially. Usually all feathers were replaced in the same year, but in a minority of birds a variable number of feathers was replaced each year, although each feather was only replaced every two years.

9. Differences are described between juvenile (grown during the nestling/fledging stage) and adult flight feathers. Adult feathers progressively replace juvenile feathers from the first adult moult in the second year of life.

10. Many juvenile wing feathers are retained at the first and some beyond the second adult moult.This has enabled a technique for age determination to be developed. A key is presented which allows tawny owls caught while breeding to be placed into four age categories.

11. In contrast to wing feathers, all juvenile tail feathers are replaced at the first adult moult.

12. The reasons for the evolution of different moulting patterns for the feather tracts were discussed. All body feathers appear to be replaced annually and this may be crucial to conserve heat. The moult of some wing feathers can be deferred for one, two or even more years, whereas tail feathers are maintained in a better overall condition by a biennial moult. Perhaps in a perch hunter like the tawny owl, the condition of primary feathers is less important than tail feathers, as tail feathers are used for steering and braking as the owls glide from perches onto prey.

CHAPTER 8

POPULATION LIMITATION

8.1 Introduction

8.2 Population trends and habitat quality

8.3 Demographic factors

8.4 Population dynamics

8.5 Summary

8.1 Introduction

In this chapter I have used data from Chapters 3 (feeding ecology), 4 (distribution), 5 (reproduction) and 6 (population turnover) to investigate which factors were responsible for limiting the size of the territorial population of tawny owls *Strix aluco* in the Kielder study area (Chapter 2). I have used data mainly from 1981 to 1991. The years 1979-80 were excluded because only part of the population was monitored, and those years were not assigned into vole year classes (Chapters 3 and 5). The methods used to collect the data are described in the relevant chapters.

8.2 Population trends and habitat quality

The number of occupied territories (Chapter 4, Table 4.5) was the best measure I had of the territorial population of tawny owls. During the study the number of occupied territories increased from 44 in 1981 to 66 in 1991. This was associated with an improvement in the habitat caused by clear-felling which increased foraging areas and food-supply (field voles *Microtus agrestis* in particular) for tawny owls (Chapter 4). However, the rise in the number of occupied owl territories lagged behind improvements in the habitat. Evidence for this came from the presence in every year of the study of apparently unoccupied territories (ranging from 2% to 22% per annum) (Chapter 4, Table 4.5), of other areas that appeared suitable for tawny owls but had never been occupied, and of areas where additional pairs might have fitted between established pairs. Hence, while the increase in the number of occupied territories tracked an improvement in the carrying capacity of the habitat, at no time did the territorial population appear to be limited by the availability of suitable habitat. The statement carries the assumption that apparently suitable habitat (some of which had been occupied in previous years) was indeed suitable in the years it was available.

8.3. Demographic factors

Tawny owls in Kielder were largely dependent on one prey species, the field vole, which exhibited a pronounced three-year cycle of

abundance (Chapter 3). Such large fluctuations in food-supply had a major influence on reproduction (Chapter 5), survival (Chapter 6) and population turnover (Chapter 6). The territorial population of tawny owls was shown to have increased by an average of 4.5% per annum which, as mentioned above, was probably below the carrying capacity of the habitat (Chapter 4). In this section I explore the role of demographic factors in limiting the population increase to below the capacity of the habitat. I have approached this by looking for factors associated with the year-to-year change in the number of occupied owl territories.

There was no indication that density-dependent factors influenced year-to-year changes in the territorial population of owls, reproduction, survival or recruitment during the 11-year period. This was not surprising as density-dependent factors were only likely to have an influence once the carrying capacity of a habitat had been reached, by regulating population change either side of an optimum. The great variation in food-supply would also have clouded any such effects if these had been present.

Reproductive success, as measured by brood size per laying pair (Chapter 5, Table 5.16), did not have any influence on percentage change in the size of the territorial population in the following year ($r=-0.132$, $n=100$, NS), which was not surprising as relatively few birds were recruited into the breeding population as yearlings (Chapter 6, Figure 6.7 upper). There was also no indication that the annual survival of territorial females (Chapter 6, Table 6.9a column E) was significantly related to the percentage change in the size of the territorial population from the previous year (Chapter 4, Table 4.5) ($r=0.450$, $n=10$, NS). Too few data from males were available to undertake similar analyses. Female survival did show a non-significant positive trend with the number of occupied territories (Chapter 5, Table 5.3 column A) ($r=0.556$, $n=11$, $P=0.076$), which probably reflected the apparent improvement in the habitat (see Chapter 6, section 6.3.6).

The only other demographic factor which could have influenced population change, was recruitment of birds into the territorial population, as there was no known emigration of established breeders. For this analysis, recruitment was calculated from the number of females breeding for the first time, expressed as a percentage of the total number of breeding females caught each year during 1983-1991 (from Chapter 6, Table 6a). Similar results to those described were obtained when the actual number of first-time breeders was used instead of percentages. Too few data from males were available to do a similar analysis, but because there was no significant difference between the sexes in natal dispersal distance (Chapter 6, Table 6.2), age of first-breeding (Chapter 6, Figure 6.7 upper) and annual survival (Chapter 6, section 6.3.6), it was unlikely that male recruitment would have been significantly different to that of females.

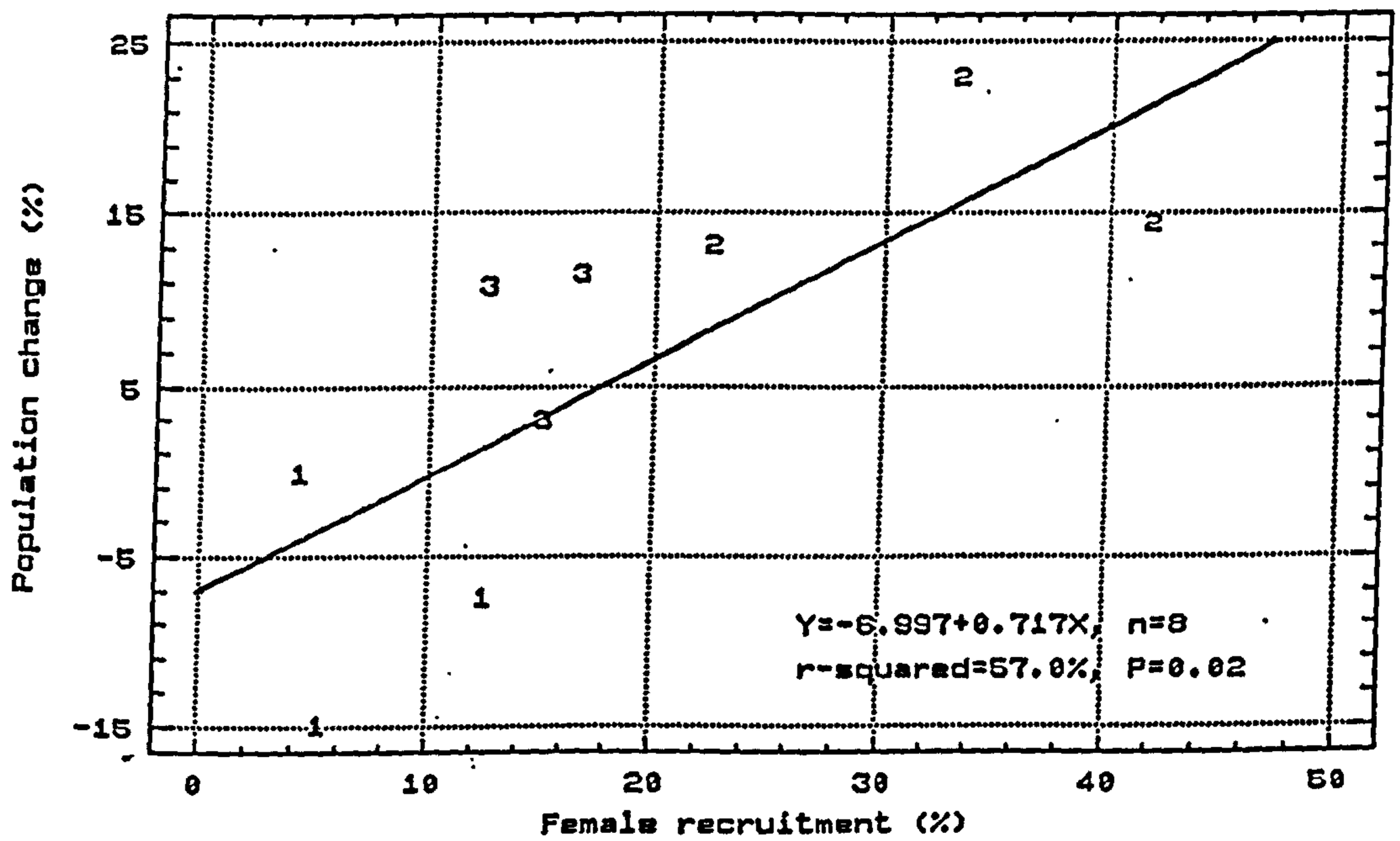


Figure 8.1 The relationship between the percentage change in the number of occupied tawny owl territories from one year to the next (y axis, Chapter 4, Table 4.5) and the recruitment of females breeding for the first time expressed as a percentage of the total number of breeding females identified (x axis, from Chapter 6, Table 6.6a). Each point represents one year classified according to vole year class (1=low, 2=increasing, 3=decreasing).

Female recruitment was significantly related to the percentage change in the number of occupied territories since the previous year (Figure 8.1). Therefore, recruitment appeared to be the most important factor influencing year-to-year change in the number of territorial birds, and hence limiting the size of the territorial population. In low vole years, less than 15% of the breeding females were new recruits, and the number of occupied territories declined (Figure 8.1). In years when vole populations were increasing, some 22%-42% of females bred for the first time, and the number of occupied territories increased by 9-24% (Figure 8.1). The vast majority of these new recruits were 3-year-olds (Chapter 6, Figure 6.7). However, in years when vole numbers started to decline, the increase in occupied territories was lower at 3-11%, with new recruits forming 13-17% of the breeding females (Figure 8.1). Most of these were yearlings (Chapter 6, Table 6.7), suggesting that virtually all of the non-breeding surplus had been recruited in the previous year when vole numbers were high. Therefore, a lack of potential recruits in increasing vole years appeared to have limited the size of the territorial population in these years. However, in declining and low vole years, surplus, non-breeding birds were present. Thus, in a declining vole year for instance, only part of the cohort produced in the previous year was recruited, and most had to wait a further two years. Perhaps in years when food was scarce (declining and low vole years), it was far better for an owl to remain in the non-territorial sector rather than incur the extra costs of defending a territory, when the chance of breeding was low. This aspect could only be clarified with a radio-tracking study.

In conclusion then, recruitment was the most important proximate factor limiting the increase in the territorial population of tawny owls. In one year of every 3-year vole cycle, the size of the territorial population was restricted by a lack of recruits, but in the other two years, when food-supply was poorer, non-breeding birds were present but failed to recruit.

8.4 Population dynamics

In any population study, it is of interest to determine whether the population is self-sustaining or dependent on net immigration to maintain numbers. In the following examination, data from females during 1980-1990 were used. Annual survival of territorial females expressed as a proportion was 0.85 (from Chapter 6, Table 6.9a) and emigration was nil. This meant that 0.15 (1-0.85) females had to be recruited locally per annum to keep the number of territorial females in balance. Overall each pair of owls (occupied territories) produced 1.63 chicks per year (Chapter 5, Table 5.25). Assuming an equal sex ratio at fledging, this represented 0.82 females chicks/pair/year of which a minimum of 14.2% (Chapter 6, Table 6.4b) or 0.12 recruits/pair/year were found to be recruited into the local breeding population, leaving a deficit of 0.03. The chicks produced in the study area represented only 61% of the new recruits into the breeding population, the remainder (39%) were unringed and assumed to be immigrants (Chapter 6, section 6.3.2) that contributed a further 0.08 recruits/pair/year (0.12/61*39). Therefore, females reared in the study area plus immigrants amounted to 0.20 recruits/pair/year, well in excess of the 0.15 females recruits/pair/year needed to keep the population in balance. This accounts for the increase in breeding numbers during the study. What was unknown was the proportion of females produced in the study area that were recruited as breeders outside the area. There were fewer data available on the demography of male tawny owls, but where comparisons could be made with females, there appeared to be no significant differences (Chapters 5 and 6).

8.5 Summary

1. In Kielder, the number of occupied tawny owl territories increased during the course of the study, while reproduction and turnover in the owl population varied greatly in response to a three-year cycle of field vole abundance.

2. The increase in the number of occupied owl territories resulted ultimately from an improvement in the carrying capacity of the habitat for tawny owls, although the increase in owls lagged behind habitat improvements.

3. To facilitate this increase, the resident territorial owl population received more recruits than was necessary to replace losses, and recruitment was the proximate factor most closely associated with year-to-year changes in the number of occupied owl territories.

4. Recruitment was also influenced by the stage of the vole cycle. In increasing vole years virtually all birds in the non-territorial sector were recruited. In low and declining vole years only some of the non-territorial owls were recruited and most deferred recruitment until vole numbers increased.

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